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Locomotion and Appendicular Anatomy in Three Soricoid Insectivores[1]

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Introduction

Anatomical studies of the present period appropriately adopt the dynamic viewpoint of the natural historian and analyze the anatomy of an animal with reference to its living conditions and activities. We may study, then, the effect of the environment, operating through natural selection, upon the genotype, which in turn determines the morphology.

The older problems of taxonomy and phylogeny are thereby related closely to the biology of the living animal. A more complete presentation of this point of view has been offered by Böker (1924), who sums up his thoughts under the term "biologische Anatomie."

There are two ways, however, in which such a study of biological anatomy is profitably pursued; one may be concerned either with closely related forms with different habits or with distantly related forms with similar habits. Thus the subject is either one of divergent or of convergent evolution. The present paper is a study of the first type. It makes use of three groups of soricoid Insectivora as materials and deals with the problem of varying degrees of fossorial adaptation.

Within the Insectivora, the shrews (Soricidae) and the moles (Talpidae) comprise a well marked superfamily, the Soricoidea (Gill, 1875). The moles,

[1] Contribution from the Museum of Vertebrate Zoölogy of the University of California, Berkeley, California.

more specialized for burrowing, were probably derived from the more generalized shrews, although Winge (1941) was of the opinion that the Soricidae developed from the Talpidae.

Of the Soricinae and the Crocidurinae, the two subfamilies of shrews commonly accepted, I had material only of the former. Of these, some genera, such as *Blarina*, are themselves semi-fossorial, so that for study I chose *Sorex* as a non-burrowing type.

The Talpidae have been divided either into two subfamilies, or into five. The older view, propounded by Mivart (1867) and discussed more fully by Gill (1875), regarded the family as composed of the Talpinae and the Myogalinae, the former more highly modified for burrowing than the latter; a technical difference between them is the possession by the Talpinae of an extra carpal bone of large size, the os falciforme or radial sesamoid. The Talpinae, using the word in this sense, are often designated the "true" moles and will be so considered in this paper.

Gill later (1888) treated the myogaline and talpine series as separate families, following the similar arrangement of Milne-Edwards (1868-1874), but this idea has not been generally accepted.

Since the generic name *Mygale* Cuvier (usually written *Myogale*) was preceded by *Desmana* Gueldenstaedt, the subfamily Myogalinae, as conceived by Mivart and by Gill, becomes the subfamily Desmaninae. The name *Desmana* is now limited to the Russian desman, the Iberian form being called *Galemys* Kaup. The details of the confused synonymy of these desmans has been presented by Miller (1912: 20-21).

Thomas (1912) divided the Talpidae into five subfamilies, the Desmaninae, Uropsilinae, Scalopinae, Talpinae, and Condylurinae, but failed to define them or, in most instances, to assign genera to them. Of these five, the first two, plus the genera *Neürotrichus* and *Urotrichus* (included in his Scalopinae) are equivalent to Gill's Myogalinae (Desmaninae) and the last two, plus the remainder of the Scalopinae, are equivalent to Gill's Talpinae. Jackson (1915) studied talpid dentition, rejected Thomas's subfamilies, and stated that if subfamilies were recognized, almost every genus would have to be assigned to a subfamily of its own.

Cabrera (1925) followed Thomas and arranged the genera of the Talpidae as follows:

Subfamily Uropsilinae: *Uropsilus, Nasillus, Rhynchonax.* (The question of whether or not *Nasillus* and *Rhynchonax* are synonyms of *Uropsilus* has not been settled; see Osgood (1937), Allen (1938), and Simpson (1945: 52).)
Subfmily Desmaninae: *Galemys, Desmana.*
Subfamily Talpinae: *Talpa, Mogera, Parascaptor, Scaptochirus.*
Subfamily Scalopinae: *Scaptonyx, Dymecodon, Urotrichus, Neürotrichus, Scapanulus, Parascalops, Scapanus, Scalopus.*
Subfamily Condylurinae: *Condylura.*

Weber (1928) recognized but two subfamilies, Desmaninae and Talpinae, as did Dollman (1929).

Winge (1941, but original in Danish, 1917) divided the Talpidae into the following groups: Nesophontini, Uropsilini, Myogalini, Urotrichi, Talpini, and Scapanei. His inclusion of the recently extinct *Nesophontes* of Porto Rico with the Talpidae has not been followed. Anthony (1916), who first described *Nesophontes*, explicitly stated that it was not related to the Talpidae.

Campbell (1939), in his paper on the shoulder anatomy of the moles, used a combination of Thomas's and Winge's classifications, with modifications of his own. He did not mention the Uropsilinae, presumably because he considered *Uropsilus* not to represent a monogeneric subfamily but to belong with the desmans; he did accept the subfamily Urotrichinae for *Urotrichus*, *Neürotrichus*, and *Scaptonyx* (with *Dymecodon*?).

Stroganov (1941) stated that Thomas's classification was "not well grounded," but seemingly proceeded to use it; furthermore, he substituted the term "Urotrichinae" in the English summary for the "Uropsilinae" of the original Russian, so that his conclusions are somewhat obscure. In a later paper (1945), Stroganov, basing his conclusions primarily on the study of the ear ossicles, listed four talpid subfamilies: the Talpinae, Scalopinae, Condylurinae, and Urotrichinae. Cabrera's Desmaninae and Uropsilinae are considered by Stroganov to be a separate family, the Desmanidae. For the four subfamilies which belong to the Talpidae as conceived by Stroganov, he mentions only those genera he studied, so that his ideas concerning the limits of each subfamily are not expressed.

Simpson (1945: 52) followed Cabrera exactly, but expressed dissatisfaction (p. 178) with the arrangement and composition of the subfamilies; particularly the Talpinae and Scalopinae, in his opinion, are not clearly natural divisions. However, the older idea of the two subfamilies as proposed by Gill he finds no more natural.

In spite of this latter conclusion, for the purposes of this study Gill's classification (1875) of two subfamilies, the Talpinae and the Desmaninae, is retained because it contrasts those moles more compeltely subterranean in habit with those only partially so.

Condylura, alone of the Talpidae, fails to fall easily into one group or the other; Dobson (1883) dissected it as a type of "true" mole in contrast to the shrew-mole group, for which he used *Desmana*. The older taxonomic works invariably listed *Condylura* with the Talpinae, as did Dollman (1929), but Winge (1941: 175) considered it as one of his Urotrichi, and Weber (1929) included it with the Desmaninae; I have followed Weber in this, but have not followed him in his inclusion of *Parascalops* in the Desmaninae.

Neürotrichus gibbsii is the only western American genus and species of the subfamily Desmaninae and hence has been used in the present work as a representative of this group. For a talpine mole I chose *Scapanus latimanus*, because I consider it representative and because it is available; however, four skeletons of *Scalopus aquaticus* were also studied.

Beyond the primary purpose of the study of fossorial as contrasted with

non-fossorial adaptations, there lay other reasons for a work of this type. Much of the anatomy of our common small mammals is unknown; this is particularly true of the Soricinae. Dobson (1882-1891) did not include the shrews in his *Monograph of the Insectivora*, and the only paper ever published primarily on soricid morphology (Ärnbäck-Christie-Linde, 1907) was based on *Crocidura*. Leche (1883) rarely mentioned any shrew other than *Crocidura* in his classic study of the pelvic musculature of the Insectivora. Campbell (1939) did, however, include some material on *Blarina* in his study of the shoulder of the moles.

Of the Desmaninae, Dobson (1883) described *Desmana* and *Condylura* in some detail, and Campbell (1939) mentioned points of interest in the shoulder of *Uropsilus*, *Galemys*, *Scaptonyx*, *Urotrichus*, *Neürotrichus*, and *Condylura*. Leche (1883) offered some notes on the pelvic musculature of *"Myogale."*

The shoulder of the true moles has fared better at the hands of the anatomists, due to the interest aroused by the extreme specialization of the fore limb, and this has been studied in some detail by several workers. Freeman (1886) made a careful study of the shoulder and upper arm of *Talpa;* Edwards (1937) published a short paper on the whole fore limb of *Scalopus;* and Campbell (1939), in the most complete paper to date, considered the shoulder and upper arm of many of the genera of the group. In addition to such studies on the fore limb, *Talpa* has been used as a basic mammalian type by Leche (1883) and by Appleton (1928) for studies of thigh musculature.

These papers are numerous, but there remains much work to do. Although the papers of Leche, Freeman, Ärnbäck-Christie-Linde, Appleton, and Campbell exhibit a high quality of anatomical research, they are limited as to the taxonomic group studied or as to the part of the body discussed, and only Campbell made any real attempt to analyze the adaptations within the groups, and then only within the limits of the shoulder and upper arm.

It is my intent, then, to describe the appendicular anatomy of a typical soricine, desmanine, and talpine more completely than has hitherto been done, to correct the errors of my predecessors, to treat statistically the osteological and myological differences in the limbs of the three subfamilies, and to correlate such differences with modes of living. The comparison of typical genera of these three subfamilies is not wholly new, since more than a century ago Brandt (1836) compared the anatomy of *Sorex*, *Desmana*, and *Talpa* in a short paper. His viewpoint was identical with that of the present writer; he considered the three genera to be related and regarded *Desmana* as an intermediate type.

Materials and Methods

There were available for dissection: six specimens of *Scapanus latimanus latimanus*, all from Berkeley, Alameda County, California; twelve specimens of *Neürotrichus gibbsii minor*, from the campus of the University of Washington, Seattle, King County, Washington; ten specimens of *Blarina brevicauda* from different parts of the eastern United States; three specimens of *Sorex*

trowbridgii montereyensis from near the lighthouse on Point Reyes, Marin County, California; and two *Mogera hainana*, from the island of Hainan, Kwantung Province, China. These latter were so poorly preserved as to be of little use except for the most superficial anatomy. Also, skins were studied of *Talpa*, *Scalopus*, *Parascalops*, *Urotrichus*, and *Condylura*, as well as those of the three genera (*Sorex*, *Neürotrichus*, and *Scapanus*) used as types for dissection; on these skins it was possible to study details of the hand and foot which would not have been available otherwise.

All skeletal materials used are in the Museum of Vertebrate Zoölogy of the University of California. Much of this material, unfortunately for my type of study, consisted of "body skeletons," of which the fore and hind feet had been clipped off and retained with the study-skin; few complete skeletons of true moles were available.

The following is a list of skeletons studied: Soricinae: 1 complete *Sorex palustris navigator*, 4 complete *S. ornatus californicus*, 2 complete *S. obscurus obscurus*, 1 complete *S. trowbridgii trowbridgii*, 6 complete *S. t. montereyensis*, 1 complete *S. jacksoni*, 1 complete *S. leucogenys*, 1 complete *S. cinereus cinereus*, 1 complete *S. vagrans vagrans*, and 1 complete *S. v. vancouverensis*.

Neürotrichus: 9 body skeletons and an articulated left fore limb of *N. gibbsii hyacinthinus*, and 5 complete *N. g. gibbsii*.

Talpinae: 2 body skeletons and 1 complete *Scalopus aquaticus machrinoides*, 1 complete *S. a. aquaticus*, 4 body skeletons of *Scapanus orarius*, 1 body skeleton of *S. townsendii*, 5 body skeletons and 1 complete *S. latimanus latimanus*, 2 body skeletons of *S. l. dilatus*, 6 body skeletons of *S. l. campi*, 3 body skeletons of *S. l. grinnelli*, 4 body skeletons of *S. l. minusculus*, 5 body skeletons of *S. l. occultus*, 1 body skeleton of *S. l. monoensis*, 6 body skeletons of *S. l. sericatus*, 1 body skeleton of *S. l. parvus*, 4 body skeletons and 2 complete *S. l. caurinus*, and 1 articulated right fore limb of *S. latimanus* subsp.

Of live material for the study of locomotor behavior I had, at different times, one *Sorex trowbridgii*, one *Neürotrichus gibbsii hyacinthinus*, and two *Scapanus latimanus*. The shrew lived only one day, but each of the other animals I kept for two weeks.

The lengths of the skull and all bones of the appendages, vertebral column, pelvic girdle, and thoracic girdle were measured with dial calipers to 0.1 mm. Usually the three dimensions of each bone were measured, as well as the lengths of the major processes; the specific measurements taken on each bone are discussed beyond in the section on osteology.

Although it was planned that the length of the vertebral column would be used as a standard length for each animal, to which standard length the remaining bones of each skeleton could be compared, this was found to be impractical because the lengths of the vertebral columns varied more than was expected. This variability resulted from two major factors: (1) the fragility of skeletons of *Sorex* and *Neürotrichus*, by reason of which vertebrae were often crushed or lost, either in trapping the animal or in preparing the skeleton; and (2) the varied techniques employed in preparing skeletons, some having been cleaned by hand, some by larvae of dermestid beetles, and some by being boiled. When boiled the vertebrae are separated and the intervertebral disks lost. Even when skeletons have all been cleaned by beetle larvae, they are bent into such a variety of positions that accurate mensuration is impossible.

It was necessary, therefore, to use the body length, as measured by the collector in the field, for a standard of comparison. This had various disadvantages, chief of which was that many of the skeletons, which had been already measured, were found to be without field measurements, so that the quantity of available data was thereby reduced. In addition, field measurements probably are not as accurate as those taken in the laboratory; indeed it was found that some animals, measured as small in the field, had skeletons larger than average, and vice versa. Extreme sets of data of this type were discarded.

Howell's (1924) observation on the inaccuracies of field measurements agree with my own conclusions. He measured two mice several times in a period of 18 hours and found a difference of 5 per cent; he assumed a further 5 per cent difference in the measurements of different collectors. There would thus be a possible range of 10 per cent in the total length and body length of each specimen as given upon the average collector's label.

To test the assumption that the body lengths, as measured, produce the high degree of variability recorded in comparisons of bone length to body length, and not the variability inherent in the lengths of the bones themselves, 24 adult skulls of *Neürotrichus gibbsii*, of three subspecies, all ages, and both sexes, were measured at random from the museum collection. Even with such a random group, the skulls themselves showed little variation in their lengths: mean, 22.3 mm. $\pm$ 0.38; σ, 0.58 $\pm$ 0.08; V, 2.61 $\pm$ 0.34. But the body lengths, as recorded for these same specimens, were highly variable: mean, 71.6 mm. $\pm$1.44; σ, 7.06$\pm$1.02; V. 9.86$\pm$1.44. Using these same 24 specimens, the percentage relationship between the skull lengths and body lengths shows a correspondingly high coefficient of variability: mean, 31.5$\pm$ 0.61; σ, 2.97 $\pm$ 0.43; V, 9.43 $\pm$ 1.36.

For each skeleton the percentage relationship was calculated between each bone and the body length, and between each bone of the limb and the length of that limb. Then, for each of the soricoid groups under consideration, these percentage values were treated statistically; the mean, the standard deviation, and the coefficient of variability, with the standard error for each, were calculated for each set of values.

Since within any one soricoid genus the relationship between any bone and the body length, or between any limb bone and the limb length could not be shown to vary with sex (often unrecorded), with age (undeterminable), with subspecies, species, or (among the Talpinae) even between genera, all the data for each genus for any one statistical relationship were grouped together. I consider this practice dependable, inasmuch as low coefficients of variability resulted from all comparisons between limb bones and lengths of limb, in which circumstances, of course, the same investigator (myself) measured both factors involved.

Animals intended for dissection were preserved in 70 per cent alcohol to which had been added a small amount of glycerin; the latter kept the specimens from drying out on the dissecting board. All dissections were made under magnifications of 8.4X, 12X, or 24X.

Except for the intrinsic muscles of manus and pes, almost every muscle was removed individually, after drawings had been finished, and preserved in 70 per cent alcohol so that the sizes of the homologous muscles in the different genera could be determined and compared. To ascertain the volume of a muscle the simple apparatus shown in figure 1 was devised. This consisted of only two parts, a 0.25 cc. tuberculin syringe and a 0.50 cc. separatory funnel, mounted together in a vertical position. The stopcock on the funnel was not needed and was left open at all times. The funnel was marked with a transverse line, and syringe and funnel were then filled to this line with 70 per cent alcohol. Any object now placed in the funnel raises the level of the alcohol, and the amount of this displacement can be determined by withdrawing the plunger of the syringe until the liquid is again at the same level in the funnel. Since the syringe is calibrated in units of hundredth of a cubic centimeter and these calibrations are of such a distance apart that they can be roughly divided into tenths with the aid of a small hand lens, the volume of the object placed in the funnel can be ascertained to 0.001 cc.

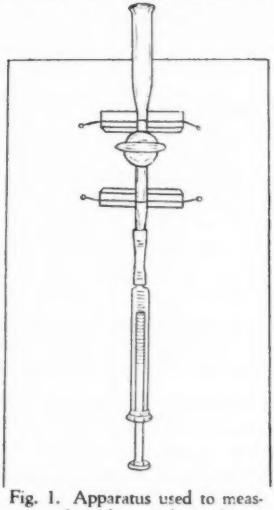

Fig. 1. Apparatus used to measure the volumes of muscles.

There are two sources of error in the volumetric mensuration of small muscles. The first is the impossibility of accurate excision of such muscles from the body; the second is that as the volumes of small muscles approach the minimum limits of mensuration of the apparatus, the percentage of error rises proportionately, until it may be 100 per cent for a muscle with a volume measured as 0.001 cc.

In the hind limb of the mole, for instance, about half of the muscles have a volume less than 0.01 cc., and in the shrew and shrew-mole most of them are so small that their individual volumes cannot be measured at all in my apparatus; thus many of the muscles of the body of these animals are of a volume less than 0.001 cc. Since I could not compare the individual muscles of the different animals, I was forced to compare muscle groups; even so, it is thought that the mensuration of the volumes of the muscles of the hind limb of *Sorex* and *Neürotrichus* was not accurate (p. 590).

For a better understanding of the skeletal changes undergone by the Talpidae in their evolution from the soricoid type, whole specimens of *Sorex* and *Neürotrichus* were cleared in potassium hydroxide and the bones stained with alizarin red. The cleared specimen of *Neürotrichus* proved particularly instructive in illustrating operation of the fore limb in the Talpidae.

Also instructive as illustrating the mode of operation of the talpid fore limb was a live, half-grown mole (*Scapanus latimanus*) which came into my possession after all dissections had been completed. This animal was first observed alive and then killed and skinned. The limbs of this young mole could be easily manipulated by hand and the effects of different muscle actions observed with an ease unknown in the study of preserved and hardened specimens.

All drawings of bones and muscles were made to scale from measurements taken with dial calipers reading to 0.1 mm.

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Locomotion

Talpine moles.—Although moles have been objects of curiosity for centuries, it is only recently that we have known accurately of their burrowing habits. Hisaw (1923) and Arlton (1936) clearly demonstrated that a mole (*Scalopus aquaticus* in each instance) neither pushes up the soil with its head and shoulders, nor, unless the soil be extremely loose, "swims" through the earth with a motion similar to that of a man swimming the breast-stroke—beliefs expressed by many writers on natural history (Kennicott, 1858; Herrick, 1892; Rhoads, 1903; and F. E. Wood, 1910, 1914). Godman (1826), although not describing the lifting action of the back and shoulders, discussed the "swimming" of the mole through the soil, as did also Mansion (1902).

The role of the mole's nose in burrowing has been variously, and wrongly interpreted. Cuvier (1817: 137) wrote that there is a special bone in the nose of the mole, *Talpa europaea*, which the animals uses for digging. Mansion (1902) mentioned the same bone in the nose of *Talpa*, but Shimer (1903) and Winge (1941: 169) stated this as if general for all moles; Winge also spoke of the mole "boring with its nose." Hornaday (1910: 57) wrote of *Scalopus aquaticus:* "Its nose sinks into the earth as if it were a brad-awl, with a combined pushing and boring motion."

I can only say that there is no special "digging" bone in the nose of *Scapanus latimanus* or *Neürotrichus gibbsii*, and I doubt if any other mole has one.

J. G. Wood ([1859]: 425) did not believe that the mole (*Talpa*) "bored" with its nose, but stated that he had observed that an individual placed on the ground "began its excavation by rooting in the ground with its nose and making a shallow groove in the earth by way of commencement. Not until it has

formed a preliminary trench does it bring its digging claws into action." Stephens (1906), although not actually believing that moles burrow with their noses, thought that in soft soil the nose is thrust ahead and that then, by pressing it to one side and the other, a cleft is formed into which the claws are thrust. From personal observations I would say that probably the nose is never thrust into the soil unless a crevice previously exists. Moreover, the claws of the mole are of such size and strength that they need no preformed opening.

Observation of a living mole impresses one with the tremendous bulk of the fore limb musculature, as compared with that of the hind limb, and with the extreme anterior placement of the fore limbs as compared with that of other mammals. Although almost all of the fore limb except the hand is drawn within the enveloping skin of the body, the fore limb is placed so far anteriorly that the hands lie alongside the head and the tips of the claws can meet in front of the nose.

These conditions result from the extremely long manubrium, which thrusts the whole pectoral girdle and limb far forward, from the very short clavicles, which pull the shoulders in close to the ventral midline, and from the fact that in the moles the humeri project dorsally from the shoulder joints instead of ventrally as in most mammals. These subjects will be discussed more fully in the section on osteology. The broad, spadelike foot, terminated by the long heavy claws, is normally extended to the side of the head, the palmar surface directed posteriorly and the medial (pollex) side of the foot rests on the ground. Thus the mole's forefoot is not basically a supportive organ, since the anterior part of the body is borne as much upon the breast as upon the hand.

Both elbow joint and wrist joint are strictly of the hinge type, permitting only anterior and posterior movement; any rotary movement or the placing of the limb in any other position must occur at the shoulder; such movement is limited, because to my knowledge the mole cannot bring its forefeet in under the body nor place either palm flat upon a level floor without rotating the whole anterior part of body so that the hand is more lateral than ventral.

The hind limbs occupy a position normal for that of small running mammals, the feet being close together and the soles flat upon the ground when not in motion. When in motion, the hind feet assume a digitigrade position. There is no such stiffness in the hind limbs as in the fore limbs, as one or both hind feet may rotate 45° or more laterally, and the hind limbs readily accommodate themselves in various ways to uneven substrates or to the curved sides of a burrow. Indeed Howell (1923), from observations on moles in "false" burrows (ones with the tops removed), stated that moles straddle the burrow with both front and hind feet; he thought such lateral bracing necessary both while digging and while running in the burrow.

This deflection of the hind limb to a semi-lateral position would seem to occur mostly at the hip, little at the knee, none at the ankle, and to some extent at the tarsal joints. No pronation or supination of tibia and fibula is

possible, as these bones are fused throughout the distal two-thirds of their lengths (fig. 10).

The established mode of digging agrees closely with these, as yet, rather superficial anatomical observations. The description of burrowing by Hisaw (1923) is the most complete and far surpasses in detail my own observations on *Scapanus latimanus;* these latter were made in a two-week period while an animal was kept in a deep, narrow, earth-filled, glass case similar to the type used by Hisaw.

Locomotion in reverse in the burrow has not been studied, although Audubon and Bachman ([1849]: 87) stated that *Scalopus aquaticus* moves backward almost as rapidly as it goes forward.

Although in loose soil the mole may "swim" through the ground, this is not the usual method of constructing a burrow. Greatest power is exerted by the mole when the fore feet are thrust out directly laterally; the mole employs its hands in this manner when digging the shallow burrows in which the soil is thrust up into a ridge. Instead of lifting the soil with back and head, as the older naturalists thought, the mole rotates in its burrow and, thrusting from below with one hand, raises the roof of the burrow with the other. Then the animal will rotate 180°, or nearly so, and repeat the process.

In excavation of deeper burrows, in which the roof cannot be elevated, only one hand is used at a time, according to Hisaw, while the other is braced against the side of the burrow. The earth is loosened by lateral strokes of first one fore limb and then the other, the earth being thrown back beside and beneath the body. After a period of this activity the mole then turns around in the newly formed burrow, the diameter of which is scarcely more than that of its own body, and proceeds to shove the dirt out, using one out-thrust hand as a pusher, with the neck and thorax bent to one side and locomotion achieved by use of the other three limbs; this same posture is maintained when pushing dirt out onto the surface. Under such conditions the hind limbs would be performing the major part of the locomotor effort.

The talpid type of burrowing, which can be termed the "lateral thrust" method, stands in contrast to that of all other mammals, which universally use the "terrier" or "rapid scratch" method, in which the animal braces itself with its hind legs and digs by means of running motions with the fore legs (Campbell, 1938). Even the South African golden "mole," *Chrysochloris,* which was long considered a talpid, burrows by the "terrier" method.

The power of the natural digging stroke of the mole is great and has been commented upon by many authors. Godman (1826) attempted a rough estimate of this power by forcing a mole to move furniture or books away from a wall, in order to find a hiding place behind them, and Audubon and Bachman ([1849]: 88) were surprised to find that a *Scalopus aquaticus* easily escaped from a wire rat trap by forcing the wires apart. The more exact experiments of Arlton (1936) indicate that the lateral thrust of the mole's fore limbs is equivalent to a lift of thirty-two times its own weight. That the mole has

stamina as well as power is indicated by the observation of Merriam (1884) that a mole (*Scalopus aquaticus*) had dug a burrow almost one hundred yards long in one night after a rain, and by the observation of Hornaday (1910: 58) that another individual of the same species burrowed 104.5 feet in the first twenty-five hours after being placed in a clover field. Bailey (1923) observed that a new surface ridge may be seen rising at the rate of a foot a minute, but the statement by Audubon and Bachman ([1849]: 88) that *Scalopus aquaticus* has been known to make in one night after a rain a fresh track several hundred yards in length is considered by me to be an exaggeration.

Out of its burrow the mole is a clumsy animal, progressing awkwardly by running with its hind legs while trying to support the heavy front part of the body on its out-thrust front legs, which are in contact with the ground only on the edge of the thumb. Its progress under such conditions is more swift than might be supposed, but relatively slow when compared with that of rodents or other insectivores of comparable size. Hanawalt (1922) recorded the top speed of *Scalopus aquaticus* as 26.7 inches per second, but he failed to state how long this was continued or whether it occurred on the surface or in the burrow; a rate of two feet per second as the top speed for *Scapanus latimanus* (Reed and Riney, 1943) when out of its burrow agrees well with Hanawalt's figure, but the recorded speed of *Parascalops breweri* as fifteen feet in thirty seconds on a smooth dirt road (Eadie, 1939) is only one fourth as fast.

There is no accurate record of the speed of any mole when within its burrow. The stated results of experiments by Le Court, a French molecatcher of the latter part of the eighteenth century, widely quoted by Saint-Hilaire and other natural historians, that a mole in its burrow runs with the speed of a trotting horse, cannot be accepted as within the physiological capabilities of the animal.

The mole seemingly cannot climb the sides of a fine-mesh wire cage, nor does it ever climb in nature. Howell (1923) found that a mole could not stand erect on its hind legs unless the fore legs were supported; my observations confirm this. A mole can, however, stretch fully erect against the vertical side of a cage and extend its fore feet to the tip of its nose; if, in this unnatural position, its claws reach the top of the cage it can pull itself up and out, demonstrating more agility than one would expect. Adams (1906) observed a captive *Talpa europaea* escape by climbing up the rough corner of its box. He returned it to the box, and reported: "I fastened some wire netting over his box. The next morning I found him actually hanging to the wire netting with his front paws, poking his nose through the meshes, and traveling from one hole to another with his body hanging perpendicularly."

The common opinion that moles never or rarely venture from their burrows is not strictly correct. They may of course be flooded out and appear suddenly above ground in some numbers. Adams (1906) caught his *Talpa europaea* in broad daylight on a meadow path. *Parascalops breweri* "apparently leaves its burrow at night and forages for food in the forest litter" (Hamilton, 1939). *Scapanus orarius* has been taken in traps at night on a bare soil surface some

distance from any burrow (Howell, 1922). Pairs of *Scalopus aquaticus* (Audubon and Bachman [1849]: 88), *Talpa europaea* (J. G. Wood [1859]: 424), and *Parascalops breweri* (Norton, 1930) have been observed fighting above ground in the daytime. In addition, Audubon and Bachman (1856: 175) observed a *Parascalops breweri* cross a gravelled road in daylight. *Talpa europaea* (Adams, 1903) comes to the surface to drink and to collect materials for its nest. Probably most talpines forage above ground more than might be suspected from the number of them observed there; evidence for this is offered by the capture of moles by hawks and owls (Fisher, 1893: 50; Adams, 1903; Cowan, 1942; Selleck and Glading, 1943).

Desmanine moles.—Of this subfamily, locomotion has been described most adequately in *Neürotrichus* by Dalquest and Orcutt (1942); their report I shall supplement with observations on the captive animal I kept myself (Reed, 1944). For locomotion in other desmanines there are only scattered references to *Condylura*. My discussion of this subfamily, then, will be almost wholly limited to *Neürotrichus*.

Neürotrichus is much smaller than any true mole, being smaller than many shrews. The fore quarters are proportionately not so enlarged as are those of the Talpinae, nor at the hands so large (fig. 7). When compared, superficially, with a mole, *Scapanus*, and a shrew, *Sorex*, the shrew-mole seems to display a blend of the characters of each, but its possession of a malar (jugal) bone and the presence of the peculiar talpid articulation between clavicle and humerus mark it clearly as belonging to the Talpidae.

Until recently little was known of this interesting small mole, and nothing of its activities. Earlier accounts concerning it (Lord, 1864; Racey, 1929) were restricted to descriptions of the burrows and the type of country inhabited. However, the survey of the biology of the animal by Dalquest and Orcutt (1942) offers much information as to locomotor abilities.

When burrowing, *Neürotrichus* proceeds with the same type of lateral strokes of the fore limbs as does a talpine mole; if placed upon a layer of soft earth it will soon disappear underground, vigorously flinging earth out to first one side and then the other side of the body. *Neürotrichus* constructs both subsurface runs and deeper, more permanent burrows. It does not, however, bring dirt to the surface to form molehills, nor does it seem to transport dirt through a burrow as will a true mole; presumably it always excavates in such soft earth that a burrow can readily be constructed by pressing the dirt aside.

Neürotrichus is much more of a hunter on the surface than is any talpine and is much more graceful and active. Due to a variety of anatomical factors, *Neürotrichus* is able to get its fore feet beneath the body, with the soles flat upon the ground. The shorter manubrium does not carry the pectoral girdle as far forward, the longer clavicles set the legs out farther from the body, the humerus projects laterally instead of dorsally, and the animal is not so "muscle-bound." The weight of the fore quarters is carried with elbow-joints projecting laterally and bent at 90° or more to reach the ground, but *Neürotrichus* can scurry to cover with surprising speed when alarmed. Although the fore feet

can be placed close together with palms applied to the ground, *Neürotrichus* must find this position tiring, as it invariably walks or runs, when above the surface, with fingers flexed, thus walking on the dorsal surface of the folded hands (Dalquest and Orcutt, 1942).

Nothing is known of the position assumed by the fore limbs of the shrew-mole when it is running through its burrow, but I imagine that the animal straddles the bottom of the burrow, with the arms extended laterally, rather than proceeding with them bent beneath the body as it does when upon the surface.

To the casual observer the hind limbs appear but little different in form and function from those of *Scapanus;* such differences of proportion as do exist will be discussed in the section on osteology. That the hind limb is capable of lateral rotation is shown in figure 2 of the paper by Dalquest and Orcutt (1942). In general the functions and abilities of the hind limb in *Neürotrichus* would seem to be closely similar to those of *Scapanus.*

Neürotrichus can rise upon its hind legs without having the fore limb supported, can climb the vertical screen of the side of a cage, or even climb into low bushes; these actions have never been observed in a true mole. The shrew-mole backs down cautiously, however, from anything it climbs, and it has never been seen to leap down, or to turn around and climb down head first, nor did I ever observe it even to turn sideways on the side of a wire cage.

The muscular power of *Neürotrichus* is not as great as that of a talpine mole. The *Scalopus* tested by Arlton (1936) lifted thirty-two times its own weight; a *Neürotrichus* tested in a similar device lifted only twenty times its own weight (Dalquest and Orcutt, 1942). Even so, it is a remarkably powerful animal.

Condylura is more fossorial than is *Neürotrichus,* but less so than any talpine (Sanborn, 1925; Hamilton, 1931; Lyon, 1936); some of the runways of *Condylura* are of the surface type, under and through marsh and meadow grass (Lyon, 1936). *Condylura* does construct molehills upon occasion (Seton, 1909: 1142), but it is semiaquatic and obtains much of its prey in the water (Hamilton, 1931). *Condylura* presumably spends some of its time hunting upon the surface of the ground; indeed Merriam (1884) found several *Condylura cristata* wandering on top of three feet of crusted snow in daylight. They had burrowed up through the snow and crust and wandered out upon the top. When approached, they tried to dig down through the crust again, but could not do so speedily enough to escape capture

Schmidt (1931) witnessed the agility of a *Condylura cristata.* He placed one in a square-cornered cement tank, of three by five feet, partly filled with water. The mole swam around until it came to a corner, whereupon it dived to seek escape. This failing, it succeeded in climbing up the two feet to the rim of the tank. Of course, in the right angle corner of a cement tank the fore feet of a mole are in a more advantageous position for support of the body than would be those of most mammals.

Presumably *Condylura* burrows with the same sort of lateral strokes as do

Neürotrichus and the talpine moles. Schmidt (1931) observed a double set of tracks on the roof of the surface burrow of *Condylura cristata* and concluded that the animal habitually brought both fore feet completely over its back with every digging stroke; I imagine, rather, that the mole was raising the roof of the burrow with one fore foot, rotating almost 180°, and raising it with the other.

Condylura approaches *Neürotrichus* in many anatomical characters, and like it can get both fore feet flat upon the ground, if the sketch of *Condylura cristata* by Seton (1909: 1144) is correct.

Sorex.—There is no written description of the locomotion of *Sorex*, perhaps because locomotion in these small shrews is thought of as "normal." It is similar to that of a small, fast mouse, except that a shrew holds its body farther off the ground. The limbs are well beneath the body, and the limb movements are of a simple fore-and-aft type; observing the animal in action one would say that the elements of any one limb move in a single plane. Cory (1912: 412) has well pictured *Sorex* in various typical poses.

The agility and activity of shrews are well known; a shrew rarely walks, but usually trots or runs. One that I had captive (*Sorex trowbridgii montereyensis*) was placed in a narrow aquarium (1⅜ in. wide) in which a litter of dead leaves, grass, and dried evergreen needles had been sprinkled to a depth of three inches over a substrate of soil. The shrew trotted back and forth over this litter for hours, hunting for the insects I dropped in. This animal often pushed down through the litter, exploring every possible small crack, but never did it show any inclination to dig down into the underlying substrate, nor did it act like *Neürotrichus* by pushing along beneath or through the litter, but always it returned to the surface.

There has been much ignorance on the part of naturalists as to the extent of the fossorial activities of *Sorex*, although most writers have assumed that these shrews do relatively little burrowing. The *Sorex* I kept, when placed in a jar containing loose earth, made no attempt to burrow, but in loose wood shavings it rapidly pushed down among them and soon disappeared. Hamilton (1940) reports on a similar experience with *Sorex fumeus*: ". . . placed smoky shrews in sizable aquaria partly filled with friable loam pressed to a consistency found in the normal habitat of these animals. Little effort was made to dig, and when the animals did try to displace dirt with their fore paws, the efforts were weak and ineffective. It seems probable that they made no burrows. . . ." Such a statement, however, as that by Soper (1923) that *Sorex personatus* is "largely subterranean in habits" would erroneously lead the casual reader to believe the animal to be a burrower. Bailey (1936: 360, 364), in speaking of *Sorex obscurus* and *S. vagrans*, stated that to some extent they make tiny burrows in the mellow woods-earth around and under old logs, but that their runways primarily are found above ground, although beneath the leaf and grass litter. With this general statement most naturalists would agree. In addition, shrews are known to use extensively the burrows of mice and moles.

Blossom (1932) kept two *Sorex cinereus* in captivity under almost natural conditions; one lived thirteen days, the other seventy-seven. He studied their habits in detail and stated that the shrews never burrowed beneath the surface, made no attempt to dig out earthworms from beneath the surface, nor even attempted to enlarge a worm hole in pursuit of an escaping worm. They would burrow, however, if placed in the unnatural location of a bare sand surface in the sun. "The action of the feet was extremely rapid, with the hind feet moving backward and outward. The forefeet were moved straight toward the rear and parallel with the body."

This description of the mode of burrowing is of especial significance to this study, as it shows that the action of a shrew, when digging, is not similar to the action of a talpid, but that the soricid mode of digging is of the "terrier" type common to all digging mammals other than the talpids. Indeed, Chamberlain (1929), in speaking of *Cryptotis parva* in captivity, stated explicitly that the animal's digging activities greatly resembled a terrier's.

The pectoral girdle of the shrew, with its long, thin clavicle articulating with the scapular acromion, precludes the possibility of the soricid exerting the type of lateral pressure which is normal to the fore limb of the talpid.

Sorex is an agile climber, running easily up the vertical screen of the side of a wire cage; it may turn sideways and may even climb along sideways or slightly downward. My captive animal never turned completely head downward, but always backed down when descending. However, Dixon (1924) recorded that *Notiosorex crawfordi* descends vertical surfaces head first by holding back with the hind feet. I never observed *Sorex* to hang suspended from, or to crawl upside down under, the wire mesh of the top of a cage, as a house mouse will do. However, *Sorex* probably climbs low bushes and inclined tree trunks in nature; *Blarina*, the eastern short-tailed shrew, is known to climb easily, even to spiral around the underneath side of a leaning tree (Carter, 1936), and *Sorex*, one would think, is certainly as gifted in this respect as is *Blarina*.

To sum up, then, with respect to the locomotor activities of these three soricoid insectivores, the shrew is purely a semi-cursorial type, the mole purely fossorial, and the shrew-mole intermediate, partaking of the characters of the other two.

Osteology

Individuals of each of the species studied by me live under remarkably uniform conditions. Therefore the muscular skills and strengths of these individuals would be expected to vary but little, and accordingly it was not considered necessary to consider the possibility that specialized skills or continuous tasks, by causing muscular hyperplasia, might create abnormal skeletal growth at the points of attachment of those muscles.

A useful premise is that both the external and internal structure of almost every bone in most vertebrates is well developed to meet the stresses to which that particular bone is subjected. Most comparative osteological study is based

upon this premise, but its truth has been demonstrated completely and mathematically, to my knowledge, for only one bone in one animal, the femur of man (Koch, 1917), but there is no reason to think that the laws of bone architecture so superbly indicated in the human femur could not as easily be demonstrated in other bones from other tetrapods.

Differences in skeletal structures of the fore limb of the shrews and moles are apparent at a glance, and have long been known to anatomists. (The only good drawings of the articulated bones, however, are by Vialleton, 1924, figs. 139-140). Yet there are many details which have received little or no attention, nor has anyone ever studied the hind limb of the same animals to establish their relative similarities and differences. Lastly, no statistical analysis of the soricoid appendicular skeleton has ever been attempted, other than a few comparisons of the fore limb by Slonaker (1920) and by Campbell (1939). In addition, there are included here similar analyses for the sacrum and the sternum, to which many of the appendicular muscles attach, and for the skull, to determine whether the latter is modified by the burrowing activities of the Talpidae.

The procedure for determining the relationship between length of each bone and the length of the body has been discussed (p. 518). After these comparisons had been made, measurements were taken of the different parts of each bone, so that the relationship could be established between the length of the bone and the length of the part. When such series of measurements are large, as they are here, and both measurements have been taken from the same specimen, one does not need to determine the percentage relationship of each measurement for each specimen, but is justified in taking the mean of the lengths of the bone and the mean of the lengths of the part and determining from these means a mean percentage relationship between the two (Engels, 1938; Simpson and Roe, 1939: 14). One does not give these figures any further statistical treatment. Of course, from this type of data there is no way of knowing when two figures, as of the proportions of bodily parts in two groups of animals, are significantly different, but in the skeletal parts under consideration the differences between the three genera are usually several times the size of any possible range of variation, or the values approach each other closely and any small differences are then considered to be without functional value.

It is true that small valid differences can thus be overlooked, but in a study of this type it is felt that if the differences between skeletal parts in different groups are small they are relatively unimportant, even though valid, and can be disregarded without loss to the major thesis.

All tabulated means are presented in percentages.

THE SKULL

To make certain that the skull of *Neürotrichus* actually is relatively longer (table 1) than are those of the other two genera, the lengths of twenty-four skulls were measured at random from the general collection of the Museum

of Vertebrate Zoölogy. When compared to the recorded body lengths of the same specimens, the mean of these twenty-four comparisons was: 31.5 ± 0.61; $\sigma = 2.97 \pm 0.43$; and $V = 9.43 \pm 1.4$. Since the cranial length of *Neürotrichus* is more than 30.0 per cent of the body length whether one uses a series of five or of twenty-four specimens, I conclude that the skull of *Neürotrichus* is relatively longer than are those of *Sorex* and *Scapanus*. I can imagine no adaptational value in this increased length of head for an animal intermediate in type between a burrower and a surface dweller.

TABLE 1.—The relationship between the length of the skull and the length of the body

	n	Mean	σ	V
Sorex	14	25.6 ± 0.5	1.75 ± 0.3	6.8 ± 1.3
Neürotrichus	5	30.3 ± 0.9	2.0 ± 0.6	6.6 ± 2.1
Scapanus	19	26.3 ± 0.4	1.75 ± 0.3	6.7 ± 1.1

To determine the general proportions of the skull, measurements of the height and breadth were taken at the greatest outside diameters. Table 2 shows the remarkable similarity of the three genera in these proportions of their skulls.

TABLE 2.—Proportions of skulls

	Height of Skull / Length of Skull	Width of Skull / Length of Skull
Sorex	29.9	49.6
Neürotrichus	31.7	46.2
Scapanus	28.7	48.2

Although a flat skull is usually considered to be a fossorial adaptation, the skull of *Scapanus* cannot be claimed to be flattened in comparison with that of the shrew, and the skull of *Neürotrichus* is the more nearly round of the three. There does not seem to be any adaptation of the skull to fit any of the animals to their environment, and one can only conjecture that the soricoid ancestor developed a shape of skull which has been inherited with but small modifications by members of both families.

THE FORE LIMB

The Mesosternum (Gladiolus).—The term mesosternum designates the sternum exclusive of the manubrium and xiphisternum. The xiphisternum may be disregarded due to its small size. The mesosternum in all three forms, in my opinion, consists of five sternebrae, as it articulates with six pairs of ribs.

If this is so the two posterior sternebrae are always fused together, so that there never appear to be more than four; sometimes the third sternebra is also fused to this posterior group. Slonaker (1920) listed three sternebrae for *Scapanus* and *Scalopus;* Bell (1839) counted five, Owen (1866: 386) four, Flower (1876: 77) five, and Freeman (1886) four sternebrae for *Talpa europaea.* I suspect such variations always are due to different degrees of fusion of the sternebrae in individual animals, an opinion in which Flower would seem to agree, as his figure 34 shows six pairs of ribs articulating with but three segments; Slonaker's figures also show a mesosternum with a similar condition.

The extremely discrepant values for V in table 3 for *Scapanus* and *Neürotrichus* are, I am convinced, entirely due to chance; since these samples were so small I recalculated the relationship of length of mesosternum to length of body for each genus from the mean of all sternal measurements and all body lengths available to me, regardless of their origin. This procedure resulted in a proportion of 7.2 per cent for *Neürotrichus* and of 9.1 per cent for *Scapanus,* values probably as true as those in table 3.

TABLE 3.—Relationship between length of mesosternum and length of body

	No.	Mean	σ	V
Sorex	11	8.6 ± 0.2	0.76 ± 0.16	8.8 ± 1.9
Neürotrichus	3	7.3 ± 0.1	0.14 ± 0.06	0.9 ± 0.4
Scapanus	4	8.7 ± 0.5	1.05 ± 0.40	12.1 ± 4.3

In general one can say that the mesosternum has not become adapted for a fossorial existence, since the values for the means in table 3 lie so close together and since the intermediate animal, *Neürotrichus,* has slightly shorter mesosternum than has either of the other two genera. The increased pectoral musculature of the Tadpidae, we shall find, comes from the manubrium and in front of it, and the more posteriorly directed force acting upon the talpid humerus by the caudal pectoral musculature occurs because of the anterior migration of the pectoral girdle and not because of any change in the mesosternum.

Manubrium (presternum).—Measurements used: (1) Length of manubrium; the total anteroposterior distance. (2) Height of manubrium; the greatest dorsoventral distance. (3) Width of manubrium; the greatest transverse distance across the wings of the manubrium.

The configuration of the manubria of a large series of soricoids (but not of *Sorex*) has been figured and discussed by Campbell (1939), so that further detailed description is not necessary. The pattern may be clearly seen in figure 2 and may be briefly described. Anteriorly there are two articular surfaces for the clavicles, followed posteriorly by two lateral processes, the wings. Behind these lie the articular surfaces for the costal cartilages of the first pair of

ribs. Posteriorly the second pair of ribs articulates with both the manubrium and the first sternebra of the mesosternum.

The manubrium of *Sorex* (fig. 2D) is much like that of *Blarina* in type (Campbell, 1939, fig. 1) but the central ridge is more pronounced and the lateral wings sharper. They both follow what is undoubtedly the general pattern for soricid manubria, although there are variations within this pattern, for in a presternum of *Crocidura russula* examined by me the lateral wings

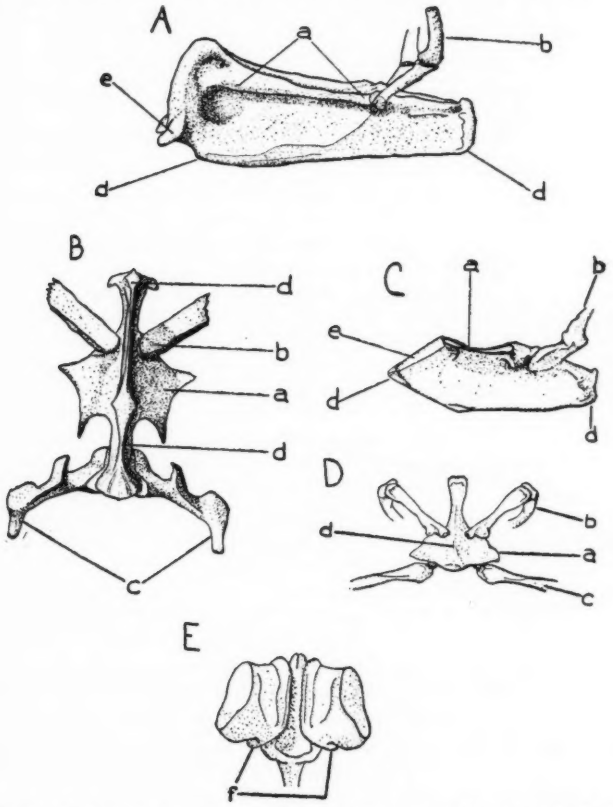

Fig. 2.—A. *Scapanus latimanus,* manubrium, lateral aspect, left side, ×2.5. B. *Neürotrichus gibbsii,* manubrium and clavicles, ventral aspect, ×5.5. C. *Neürotrichus gibbsii,* manubrium, lateral aspect, left side, ×5. D. *Sorex vagrans,* manubrium, ventral aspect, ×5. E. *Scapanus latimanus,* manubrium and clavicles, anterior aspect, ×2.5. a, wing of the manubrium; b, first rib; c, clavicle; d, keel of the manubrium; e, area on manubrium for articulation with clavicle; f, tubercle of the clavicle.

were shorter and narrower than in *Sorex*, so that the first rib articulated closer to the clavicular articulation.

The manubrium is relatively twice as long in *Neürotrichus* as in *Sorex* and three times as long in *Scapanus*. The increase in length has been almost entirely anterior to the point of articulation of the first rib, so that the relative position of the first rib remains practically unchanged throughout the group.

TABLE 4.—Relationship between length of manubrium and length of body

	No.	Mean	σ	V
Sorex	13	4.1 ±0.1	0.45±0.1	10.8±2.1
Neürotrichus	11	8.75±0.1	0.4 ±0.1	4.9±1.0
Scapanus	23	12.6 ±0.1	0.65±0.1	5.1±0.8

It is interesting that the lateral wings of the manubrium are wide in *Sorex* (table 5), where they have little muscular attachment, and narrow in *Scapanus*, where they furnish origin on each side to a pair of strong muscles (M. costoscapularis ventralis), which muscles are lacking in *Sorex*. In *Neürotrichus*, where the wings also furnish origin to this pair of muscles, they are actually wider than in *Sorex*, although appearing to be relatively less so due to the increased length of the manubrium in *Neürotrichus*. In *Scapanus* the reduction in width is both actual and relative. There appears to be but little relationship in this particular instance between myological and osteological morphology.

TABLE 5.—Proportions of Manubrium

	Width of Manubrium / Length of Manubrium	Height of Manubrium / Length of Manubrium
Sorex	86.6	22.3
Neürotrichus	66.7	33.8
Scapanus	18.0	34.3

A more important fossorial adaptation is the tremendous deepening of the keel in the Talpidae. Since the keel gives support to the greater mass of the pectoral musculature, several components of which are absent in *Sorex*, increase in surface is a function of the increase in volume of the muscles in the fossorial forms. Although the keel in *Neürotrichus* is, when compared to the length of the manubrium, relatively as deep as in *Scapanus* (table 5), the lateral surface is relatively much less, not only because the presternum is relatively shorter in *Neürotrichus*, but also because the keel tapers anteriorly and posteriorly, whereas in *Scapanus* it better maintains its depth throughout its length (compare figures 2A and 2C).

In considering the manubrium there are therefore two important series of

adaptive changes with close correlation between locomotor habits and skeletal differences: (1) the increased length with greater fossorial activity; (2) the increased lateral area, for attachment of much of the pectoral musculature, with increased fossorial activities. The decrease in width of the wing with the increase in fossorial activity cannot be satisfactorily interpreted.

Clavicle.—Measurements used: (1) Length of clavicle; the distance from the middle of the proximal articular surface to the middle of the distal articular surface. (2) Height of clavicle; in *Sorex*, the dorsoventral height measured midway along the length of the bone; in the Talpidae, the narrowest dorsoventral height, which is near the proximal end. (3) Thickness of clavicle; the anteroposterior distance, measured at right angles to the height of the clavicle.

TABLE 6.—Relationship between length of clavicle and length of body

	No.	Mean	σ	V
Sorex	14	7.5 ± 0.1	0.4 ± 0.1	5.9 ± 1.1
Neürotrichus	11	4.7 ± 0.1	0.25 ± 0.05	5.3 ± 1.1
Scapanus	24	2.6 ± 0.4	0.2 ± 0.03	7.85 ± 1.1

The talpid clavicle is markedly different from that of any other vertebrate in two ways: (1) it is extremely short and heavy; (2) distally it articulates with the greater tuberosity of the humerus instead of with the acromion of the scapula. The shortness allows the fore limb of the talpid to maintain nearly its same relative length as compared to *Sorex* and yet work in the confining limits of a burrow; thus the clavicle has become progressively shorter in the more fossorial forms (table 6; Campbell, 1939; Kistin, 1929).

The talpid clavicle has by most authors been considered simply as a true clavicle, but it is so different in the adult from that of any other mammal that it has been thought by Vialleton (1924: 296, 299-303) to be a coracoid, and by W. K. Parker (1868: 212) to be a coraco-clavicle; T. J. Parker and Haswell (1897: 518) termed it a procoraco-clavicle and coraco-clavicle in the same paragraph; in their sixth edition (1940: 549) they again called it a procoraco-clavicle. Flower (1876: 227), following W. K. Parker, considered that the bone might represent a coraco-clavicle, as did Freeman (1886).

Theoretically the origin of the mole's clavicle should be no different from that of any other monodelphian mammal. Hanson (1920) summarized the literature in this field and his own investigations on the development of the clavicle of man and of the opossum. He concluded that the therian clavicle ossifies in two centers from a peculiar and distinctive tissue which is not hyaline cartilage; he regarded the clavicle as completely a dermal bone. Zumpe (1925), who did not quote any recent work in English, assumed a contrary position from an investigation of the developing clavicle of *Talpa europaea*. He found that the clavicle of the mole ossifies from two centers, one cartilaginous and

one dermal; the cartilaginous he termed a "procoracoid" element. He found also that the embryonic clavicle first articulates with the acromion, but that the distal part then degenerates to form the acromioclavicular ligament. The subject has been reinvestigated in the Talpinae by Kistin (1929), who did not, however, cite pertinent literature in the field. Kistin used embryological and comparative anatomical evidence to show that the bone is not a coracoid, but he did not prove, as he assumed he did, that it is wholly a clavicle.

Far from indicating a condition which must be explained by the retention of reptilian pectoral bones otherwise lost in therian mammals, the evidence indicates to me that the humeral articulation of the clavicle has developed naturally. In the shrew the long, thin clavicle projects laterally and then dorsolaterally to articulate with the acromion; the clavicle passes so close to the glenoid fossa that there is a secondary articulation with the coracoid process. The articulation of the head of the humerus with the glenoid fossa brings the greater tuberosity of the humerus close to the distal end of the clavicle (fig. 3C); if the humerus were then to extend laterally the greater tuberosity would be swung dorsally and medially so that it would come in contact with the distal end of the clavicle. Such an alignment would add immediate support to the joint between humerus and pectoral girdle, especially supporting medial thrusts transmitted through the long axis of the humerus.

This intermediate condition, of a clavicle articulating with both acromion and greater tuberosity, is still retained by the most primitive talpid, *Uropsilus*, according to Campbell (1939, fig. 21). This was the first time, to my knowledge, that this primitive, intermediate condition of the shoulder-joint of *Uropsilus* was noticed, and it is hardly possible to over-emphasize its fundamental importance in the understanding of the evolution of the talpid shoulder-joint. It is curious that Winge (1941: 172) stated that there is no articular surface between the clavicle and the humerus of *Uropsilus;* however, Campbell's figure is clear upon this point and Winge's statement can be discounted.[1]

From the primitive condition as found in *Uropsilus* the shoulder-joint of the remainder of the desmanines has developed by loss of the cleidoscapular articulation, and the talpine shoulder-joint has developed from the desmanine type by concomitant growth of the greater tuberosity, a more dorsal elevation of the distal end of humerus, and shortening and thickening of the clavicle.

The clavicles of *Blarina* and of a large series of talpids are figured and described by Campbell (1939) and the clavicle of *Scalopus aquaticus* has been figured and described in detail by Edwards (1937), so that further description is not here necessary, since the clavicle of *Sorex* is shown in figures 2D and 3C, that of *Neürotrichus* in figure 2B, and that of *Scapanus* in figure 2E.

The enormous differences in the proportions of the clavicles of the three genera are at once apparent from tables 6 and 7; in *Sorex* the clavicular length is eighteen times its height, in *Neürotrichus* it is two and one-half times its

[1] Since this was written the author has had opportunity to view a skeleton of *Uropsilus*, and finds Campbell's statement and figure to be correct.

height, and in *Scapanus* the length is only three-fourths of its height. While the anteroposterior thickness of the bone does not increase so remarkably, yet noteworthy are the great increases in massiveness of the clavicle of *Neürotrichus* as compared to *Sorex* and of *Scapanus* as compared to *Neürotrichus*.

The correlation between the burrowing habits of the animals and the mechanical strengthening of the clavicle is obvious.

TABLE 7.—Proportions of Clavicle

	Height of Clavicle / Length of Clavicle	Thickness of Clavicle / Length of Clavicle
Sorex	5.5	6.9
Neürotrichus	39.5	18.05
Scapanus	131.2	61.6

Scapula.—Measurements used: (1) Total length; the distance from the tip of the vertebral border to the shallowest point on the rim of the glenoid fossa. (2) Width of vertebral border; the greatest width of the scapula. (3) Height of tubercle; the distance from the highest point on the scapular spine to the point immediately opposite on the subscapular surface. (4) Length of the infraspinatus fossa; since the ends of the fossa are not sharply delimited, this distance cannot be accurately measured; however, every effort was made to measure all in as nearly an identical manner as possible, and the differences between the three genera are great enough so that small errors of mensuration could not seriously disturb the final result.

The scapula is markedly elongated in the Talpidae, as compared with the Soricidae (table 8), but not necessarily narrowed (table 9), as that of *Neürotrichus* is wider in one place in proportion to its length than in either *Sorex* or *Scapanus*. In general appearance the scapulae of *Sorex* and of *Neürotrichus* are fragile, while that of *Scapanus* is comparatively heavy and rugged (fig. 3).

TABLE 8.—Relationship between length of scapula and length of body

	No.	Mean	σ	V
Sorex	14	9.1 ± 0.2	0.64 ± 0.1	7.1 ± 1.3
Neürotrichus	11	16.6 ± 0.24	0.8 ± 0.2	4.85 ± 1.0
Scapanus	21	17.5 ± 0.2	1.0 ± 0.15	5.6 ± 0.9

The scapulae of the two families occupy very different positions on the dorsolateral surface of the thorax; the long axis of the scapula of *Sorex* is almost vertical, that is, almost perpendicular to both the ground and to the spinal column, so that the axillary (glenoid) border is posterior, the coracoid (superior) border anterior, the vertebral border dorsal, and the glenoid fossa

ventral but facing slightly forward. The long axis of the scapula of *Scapanus* or of *Neürotrichus* runs anteriorly, somewhat ventrally, and slightly laterally; the M. spinodeltoideus (fig. 26) follows the scapula closely.

This rotation of the scapular axis is approximately 60° from the soricid to the talpid condition and would seem to be correlated primarily with the lengthening of the talpid manubrium and the shortening of the talpid clavicles, which project the shoulder-joints far forward and close together under the head. If the scapular axis in a talpid remained at nearly a right angle to the long axis of the body, the scapula would project dorsolaterally from the side of the head. Undoubtedly there have actually been other considerations, such as the changed myological relationships between scapula and humerus and between scapula and olecranon, which have influenced the position of the posterior end of the scapula, which varies little in the three forms, but lies at the level of the fifth or sixth rib.

The glenoid fossa shows important differences between the soricids and the talpids, correlated with the differences in shapes of humeral heads and positions of the humerus. In *Sorex* the glenoid fossa is a segment of a spherical surface and allows movement of the spherical head of the humerus to occur freely in all directions. In *Neürotrichus* and *Scapanus* the articular surface of the glenoid fossa is an ellipse, the long axis of which lies at an angle of 70° with the plane of the subscapular surface. In the position assumed by the scapula on the side of the thorax the long axis of the glenoid fossa lies as indicated in figure 4.

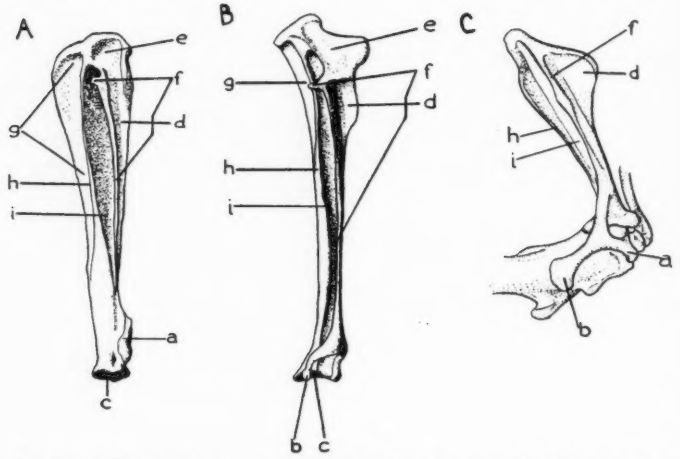

Fig. 3.—A. *Scapanus latimanus*, right scapula, dorsal aspect, ×2.15. B. *Neürotrichus gibbsii*, right scapula, dorsal aspect, ×4.2. C. *Sorex obscurus*, right scapula and shoulder-joint, dorsal aspect, ×4.2. a, acromion; b, metacromion; c, glenoid fossa; d, supraspinatus fossa; e, rhomboid area; f, spine; g, teres fossa; h, axillary border; i, infraspinatus fossa.

The change in the long axis of the glenoid fossa from soricid to talpid has been mostly a change in the configuration of the fossa, but it has been accompanied by some twisting of the neck of the scapula; at least the base of the talpid acromion does seem to have been shifted slightly mediad and ventrad from its position in *Sorex*.

The long axis of the glenoid fossa lies at approximately the same angle to the body and to the substrate in both *Neürotrichus* and *Scapanus*. There is no factor here, then, to account for the differences in the angles at which the humeri lie in the two genera.

The reduction of the acromion and metacromion processes in the more fossorial talpids was noted by Campbell (1939), who presented drawings of a large series of talpid scapulae to illustrate this point. However, his drawing of the scapula of *Neürotrichus* is inaccurate, inasmuch as he showed it with a reduced metacromion, whereas there is actually present a high, delicate process. The reduction of the metacromion-acromion is correlated with the disappearance of the M. atlantoscapularis anterior in *Neürotrichus* and the lack of this muscle and of the M. trapezius anticus in *Scapanus;* in turn, the disappearance of these muscles is associated with the shortening of the clavicles, the increased strength of the humeralclavicular joint, and the consequent more solid anchoring of the anterior end of the scapula in the more fossorial forms.

The infraspinatus fossa of *Sorex* (fig. 3C) runs nearly the entire length of the scapula and is bounded posteriorly by the high rim of the axillary border, so that the fossa is relatively deep and narrow. The scapula of the talpids has developed further from the soricid condition and is unique among mammals in that the normal axillary border has moved up onto the dorsal surface, constricting the infraspinatus fossa to a deep, narrow gutter, which is consistently shorter and narrower in the more fossorial forms, until in *Talpa* and *Mogera* the axillary border fuses with the spine and the infraspinatus fossa is obliterated (Campbell, 1939). This development of the scapula is accomapnied by the reduction and finally the disappearance of the M. infraspinatus, which is otherwise found continuously throughout the mammalian series (Howell, 1937b). The beginning of the process of fusion between spine and axillary border is seen at the vertebral end of the scapula in *Scapanus,* where such fusion roofs the vertebral end of the infraspinatus fossa and converts it into a cave. Freeman (1886) called the teres fossa of *Talpa europaea* the infraspinatus fossa, since he never realized that the latter had disappeared.

TABLE 9.—Proportions of Scapula

	Infraspinatus length / Scapular length	Height of spine / Scapular length	Width of vertebral border / Scapular length
Sorex	91.5	26.8	26.8
Neürotrichus	84.1	14.8	27.5
Scapanus	58.2	14.0	22.2

Although the relative reduction in the height of the tuberosity of the scapular spine (table 9) in the Talpidae can be attributed to the greater length of the scapula, there has nevertheless been a definite, even extreme, reduction of the spine with increase in fossorial activity. In *Sorex* the spine is continuously high throughout the length of the bone, but in *Neürotrichus* and *Scapanus* it falls away rapidly on both sides of the tuberosity; in *Neürotrichus* it rises again into a high metacromion, but in *Scapanus* it is obliterated entirely at both ends of the infraspinatus fossa and rises again only in a low bump at the acromion.

The supraspinatus fossa is remarkably small in the Soricinae and Talpidae, but the M. supraspinatus takes origin from the side of the spine as well as from the fossa, and in the Talpidae it takes origin also from the M. subscapularis, so that the size of the fossa is not an indication of the size of the muscle.

In *Neürotrichus* there is a rhomboidal area set off from the suprascapular fossa at the vertebral end of the scapula; in *Scapanus* these surfaces are continuous. Since the rhomboidal area does not serve for muscular attachment, there would seem to be no functional explanation for this difference in morphology.

The so-called "teres fossa" is not represnted in *Sorex*, but it is presumably present in all talpids except *Uropsilus* (Campbell, 1939). It does not, however, serve as an area of origin for the M. teres major in *Neürotrichus* as Campbell has labeled it, but is for a separate head of the M. subscapularis. In *Scapanus*, however, and presumably in all Talpinae, the fossa gives origin to the greatly hypertrophied M. teres major.

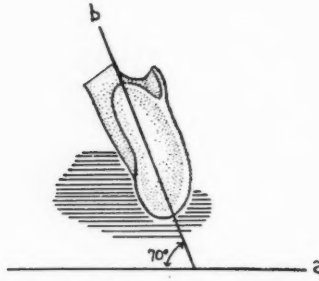

Fig. 4.—Right scapula, *Scapanus* or *Neürotrichus*, anterior view; a, plane of the subscapular surface; b, long axis of the glenoid fossa.

The coracoid process is prominent in *Sorex* and *Uropsilus*. In most talpids, however, it is reduced completely; Parker (1868: 211) believed the scapula to be without any coracoid representative, since he thought the coracoid fused completely with the clavicle. I do not know of any functional significance that can be associated with the reduction of the coracoid process.

Although the vertebral borders of the scapulae in the three genera differ remarkably in configuration, again I do not know of any functional differences that can be correlated. Within the genus *Neürotrichus* this border may vary from concave to convex, and these variations certainly cannot have functional significance; figure 3B illustrates one of the more concave examples.

The subscapular surface in all is slightly concave at the widest point, but the scapula of each becomes columnar in shape as the glenoid fossa is approached.

The belief, commonly accepted, that the scapulae of burrowing forms tend to be narrower than those of their non-burrowing relatives is borne out by the genera being studied. In spite of the fact that the vertebral border of *Neürotrichus* is relatively as wide or wider than that of *Sorex* (table 9), the greater part of the scapula of *Neürotrichus* is round and narrow, with the infraspinatus fossa converting it into a hollow column open on one side.

Humerus.—Measurements used: (1) Total length; the distance from the most proximal point on the humerus to the center of a line between the two most distal points. (2) Proximal width no. 1; the distance across the greater and lesser tuberosities, measured at right angles to the long axis. (3) Proximal width no. 2; the greater distance between the teres tubercle and the greater tuberosity, measured at right angles to the long axis. (4) Distal width; the greatest width across the lateral and medial epicondyles, measured at right angles to the long axis. (5) Head thickness; the distance from the most posteriorly projecting point on the head, through the humerus at right angles to the long axis, to the nearest point on the opposite (anterior) surface. (6) Length of teres tubercle; the distance from the most proximal point on the humerus to the distal tip of the teres tubercle, measured on a line parallel with the long axis. (7) Shaft width; the narrowest mediolateral distance across the shaft of the humerus, measured at right angles to the long axis. (8) Shaft thickness; the anteroposterior distance from surface to surface, measured at the same level as, and at right angles to, the shaft width. (9) Length of greater tuberosity; the distance from the most proximal point on the humerus to the most distal point on the greater tuberosity, measured parallel with the long axis of the humerus. This measurement is not strictly comparable between the two families, as in *Scapanus* and *Neürotrichus* it includes the length of the deltoid process, whereas in *Sorex* it does not. (10) Length of lesser tuberosity; the distance from the most proximal point on the humerus to the most distal point on the medial periphery of the lesser tuberosity, measured parallel with the long axis of the humerus. (11) Medial epicondylar length; the distance from the most proximal tip of the medial epicondyle to the most distal point on the medial side of the humerus, measured parallel with the long axis. (12) Lateral epicondylar length; the distance from the most proximal tip of the lateral epicondyle to the most distal point on the lateral side of the humerus, measured parallel with the long axis.

Probably no mammalian bone shows greater agreement between form and function than does the soricoid humerus, and unless one follows through a soricoid series one would be puzzled by the homologies of the parts of the talpine bone, so strongly has it been molded. Major errors in osteological nomenclature have been committed in the past due to attempts to study the mole humerus as an isolated entity without regard to its evolution.

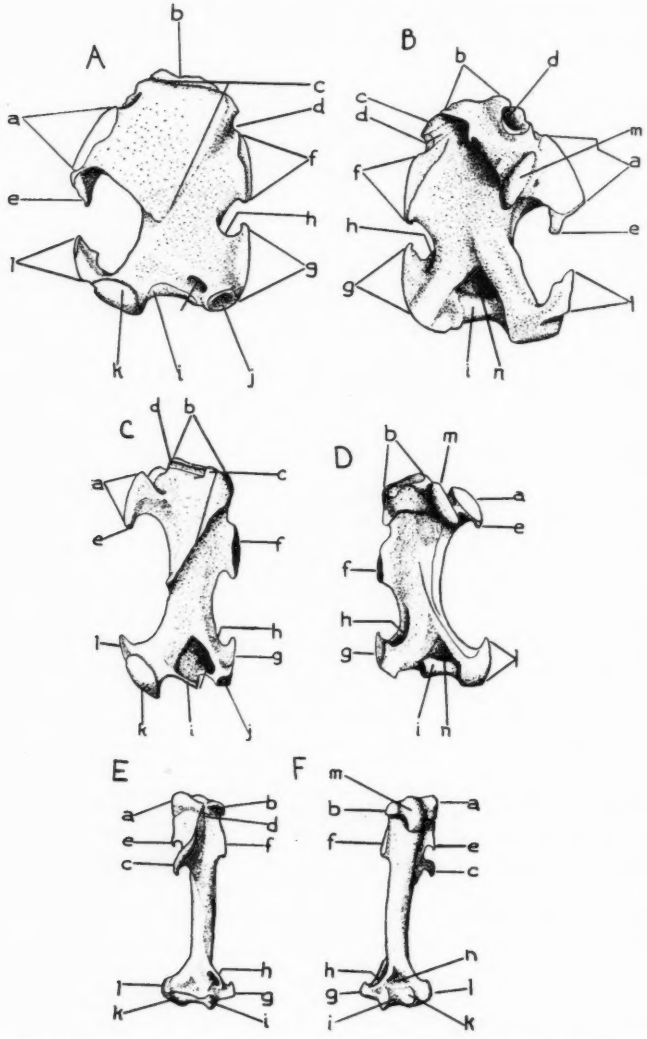

Fig. 5.—A. *Scapanus latimanus*, right humerus, anterior aspect, ×2.3. B. Posterior aspect of A, ×2.3. C. *Neürotrichus gibbsii*, right humerus, anterior aspect, ×4.65. D. Posterior aspect of C, ×4.65. E. *Sorex trowbridgii*, right humerus, anterior aspect, ×4.65.

TABLE 10.—Relationship between length of humerus and length of body

	No.	Mean	σ	V
Sorex	15	10.4 ±0.2	0.7±0.13	6.9±1.3
Neürotrichus	11	10.2 ±0.2	0.5±0.1	5.2±1.1
Scapanus	20	10.85±0.1	0.6±0.1	5.4±0.85

The common statement that the humerus of the mole is "short" (Flower, 1876: 249; Dobson, 1883: 163; Freeman, 1886; Flower and Lydekker, 1891: 633; Dollman, 1929; Arlton, 1936; Edwards, 1937) is not accurate; it merely looks short due to its great breadth. Actually the lengths of the humeri of the three genera (table 10) are remarkably similar, although the functional length in the more fossorial forms has been reduced, due to the migration of the head from the proximal end in the shrew onto the posterior surface in the shrew-mole and mole.

In no other mammalian group has the humerus undergone such a remarkable shift in position in the body as it has in the Soricoidea. In *Sorex* the bone occupies the same position as it does in a dog, moving in a fore-and-aft plane. When extended, the humerus projects slightly anteriorly and toward the ground; when retracted, the humerus is parallel with the body and points posteriorly. In *Neürotrichus* the humerus has shifted from this soricine position until it points laterally when normally extended; in retraction the bone moves in a lateral plane onto the thorax. In *Scapanus* the bone has shifted somewhat further in position, until it points laterodorsally, so that the distal end lies beside the skull.

The difference in position between the humeri of *Sorex* and the two talpids is due to the facts that in the talpids the head of the humerus has become elliptical, has shifted to the posterior surface of the humerus, and fits snugly into the elliptical concavity of the glenoid fossa. The difference in position between the humeri of *Neürotrichus* and *Scapanus* is caused by a difference in the angles between the long axes of the humeral heads and the long axes of the humerus in the two genera. The long axes of the glenoid fossae of both genera, it is to be remembered, point laterally and slightly dorsally. The long axis of the head of the humerus of *Scapanus* points mediodistally from the long axis of the humerus at an angle of about 20°; the long axis of the head of the humerus of *Neürotrichus* points laterodistally at an angle of about 25° from the long axis of the humerus (compare figs. 5B and 5D). Since each of

F. Posterior aspect of E, ×4.65. a, greater tuberosity; b, lesser tuberosity; c, pectoral process; d, bicipital groove; e, deltoid process; f, teres tubercle; g, medial epicontyle; h, supracondyloid (entepicondylar) foramen; i, trochlea; j, fossa for origin of great ligament of the M. flexor digitorum profundus; k, capitulum; l, lateral epicondyle; m, head; n, olecranon fossa.

these heads fits into a glenoid fossa of the same shape and position, the humerus of *Scapanus* must project from the body at an angle of approximately 45° more dorsally than does the humerus of *Neürotrichus*, and it does so. This explanation of the variable positions assumed by the humeri of talpid genera has never before been advanced, but would be valid, in my opinion, for all talpid genera except *Uropsilus*, the humerus of which does not possess an elliptical head (Campbell, 1939, fig. 39).

The joint between the head of the humerus and the glenoid fossa allows of movement in but one plane, that of retraction and extension; any raising or lowering of the distal end of the humerus can be accomplished only by a rotation of the scapula. That such movement is limited, especially in the Talpinae, is indicated by the fact that no true mole can depress the humerus enough to bring its fore feet beneath the body.

The change in position of the talpid humerus leads to confusion in the naming of the borders. The anterior and posterior surfaces remain theoretically the same as in the shrew (compare the identical views of figure 5), but the medial and lateral surfaces, which in the shrew are normal for mammals, change to ventral and dorsal, and to lateral and medial, respectively, in shrew-mole and mole, as the distal end of the humerus becomes more and more elevated. For the sake of consistency I will retain the terms "lateral" and "medial" in the sense in which they apply to the shrew, so that the greater tuberosity and the lateral epicondyle, for instance, are always on the "lateral" side of the humerus, no matter what position they may assume in the body.

Failure to realize these changes in position have led to some remarkable errors in the literature. Thus Owen (1866: 391) called part of the pectoral ridge the deltoid ridge and named the teres tubercle the pectoral ridge. Flower (1876: 249) mistook the teres tubercle for the deltoid ridge. Dobson (1883, footnote, p. 163) corrected Owen's errors, but could not stop the tendency. Slonaker (1920, fig. 8) called the greater tuberosity the head of the humerus, the deltoid process the lesser tuberosity, the lesser tuberosity the greater, and the teres tubercle the deltoid process. In his comparison of the humeri of *Talpa* and *Galemys*, Puisségur (1935, figs. 64, 65) labeled the teres tubercle as the greater tuberosity and confused the identity of the medial and lateral epicondyles. Edwards (1937) thought the proximal lateral border of the humerus of *Scalopus* to be the deltoid ridge and considered the true deltoid process to be merely a part of the greater tuberosity. Winge (1941: 168) mistook the proximal part of the pectoral ridge for the deltoid process.

Confusion of the major parts of the humerus of the mole is really inexcusable, as over a century ago Bell (1839) accurately identified the larger surfaces, and later Freeman (1886) correctly designated the major processes, failing only to recognize the deltoid process, which he termed merely a "hook-like" process.

The joint formed in the Talpidae between the rounded surface of the greater tuberosity and the rounded depression at the distal end of the clavicle

has already been discussed (p. 534). It need only be added that the surface on the humerus is somewhat larger than the corresponding face of the clavicle, indicating rather extensive movement by the humerus, as was first noted by Slonaker (1920); such movement is necessarily limited, by the joint between humeral head and glenoid fossa, to retraction, extension, and rotation of the humerus. Slonaker (1920) miscalled the greater tuberosity the head of the humerus and quite obviously regarded the true head as a new acquisition.

The bicipital groove, through which passes the tendon of origin of the M. biceps brachii, is seen at its simplest in *Sorex* (fig. 5E); it has the same character in *Uropsilus* (Campbell, 1939). In these forms the groove lies on the anterior face of the humerus, between the pectoral ridge and the teres tubercle, as Campbell stated, but more important to its future development, the proximal part of it lies between the lesser tuberosity and the proximal end of the pectoral ridge.

In *Neürotrichus* (fig. 5C) there is clearly seen the mode of formation of a primitive bicipital groove into the typical closed tunnel of the talpid. The widening of the proximal end of the humerus of *Neürotrichus* is caused by a transverse growth of the lesser tuberosity, while the greater tuberosity and the head have moved more onto the lateral and posterior surfaces, respectively. This transverse growth of the lesser tuberosity would, in itself, merely displace the biceps tendon laterally, were it not that the proximal part of the pectoral process has increased to such size that the biceps tendon cannot ride over it, but must pass mediad to it; indeed the proximal part of the pectoral ridge (called by Dobson the bicipital ridge and by Campbell the pectoral crest) and the lesser tuberosity meet above the tendon and form the biceps (bicipital) tunnel. *Neürotrichus* has already begun the process of transverse growth of the pectoral crest which is completed in the talpines to form a longer bicipital tunnel across the proximal end of the humerus (figs. 5A and 5B).

In *Scapanus,* as in all talpines, the process of formation of the bicipital tunnel appears to have reached its ultimate possibility; indeed, the medioproximal angle of the pectoral process has grown medially farther than has the lesser tuberosity (fig. 5B), so that a part of the bicipital groove appears to lie on the posterior surface of the humerus; actually this portion of the bicipital groove is occupying the original medial surface of the pectoral ridge, which now lies parallel with and proximal to the teres tubercle. To regain its normal position on the anterior surface of the humerus the biceps tendon traverses the bicipital notch (fig. 5B) between the teres tubercle and the pectoral crest.

Thus it is shown that the bicipital tunnel, peculiar to talpids, is formed between the lesser tuberosity and the proximal part of the pectoral ridge. Dobson understood this, and described it for *Desmana* (1883: 147), but his subsequent use of the term "bicipital ridge" when describing *Condylura* and the talpines (1883: 163) confused the issue, and Edwards (1937) assumed the bicipital tunnel of *Scalopus aquaticus* to have been formed by two lamellae of the lesser tuberosity.

The more distal part of the pectoral ridge becomes proportionately reduced in height as the animals become more fossorial. This ridge serves as insertion for the M. pectoralis superficialis anticus, which becomes proportionately larger in the more fossorial animals, and one might expect the muscle attachment to grow with the muscle; actually it does grow in length.

The deltoid area, the quadrilateral surface between the pectoral ridge and the greater tuberosity, enlarges with the broadening of the humerus and the distal growth of the pectoral ridge, but minor changes of topography within the area do not seem to have any functional significance. In *Sorex* and *Neürotrichus* the area is crossed by the Mm. cleidodeltoideus and acromiodeltoideus, which insert upon the pectoral ridge, but in *Scapanus* the M. acromiodeltoideus fails to reach the ridge; instead, a slightly raised and roughened surface of the distal angle of the deltoid area marks its insertion.

The deltoid process (also called ridge or tuberosity) has hitherto been overlooked or misnamed in the Talpidae. Owen (1866) and Dobson (1883) ignored it; Freeman (1886) called it a "hook-like process"; Edwards (1937) defined the deltoid tuberosity as the border of the humerus between the greater tuberosity and the distal end of the pectoral ridge; the true deltoid process he regarded as merely a projection from the greater tuberosity. Campbell (1939) called it an "uncinate process" on the greater tuberosity. The true status of the deltoid process is more understandable when it is seen in the shrew to be a short ridge on the lateral shaft of the humerus distal to the greater tuberosity, a position normal for mammals. The M. spinodeltoideus inserts on the distal part of this ridge. In *Neürotrichus*, with the hypertrophy of the greater tuberosity, the deltoid process has been reduced to a small nubbin upon the periphery of the tuberosity, overhanging the brachialis fossa; the M. spinodeltoideus, however, inserts upon it as in *Sorex*. In *Scapanus* the deltoid process is larger than in *Neürotrichus*, but occupies the same relative position and serves as the point of insertion for the same muscle.

In *Sorex* the greater tuberosity merely overhangs the shaft of the humerus, but in *Neürotrichus* the posteromedial portion of the greater tuberosity possesses an internal concavity, the brachialis fossa, which gives origin to the superficial head of the M. triceps lateralis and, in part, to the M. brachialis anticus. In *Scapanus* this concavity has enlarged to a deep, hollow cone, the apex of which nearly penetrates the proximal surface of the greater tuberosity. Most of this cavity serves for the origin of the M. brachialis anticus.

The tubercle to which attach the Mm. latissimus dorsi and teres major has never received a specific name in mammalian anatomy. In man it is known as the "crest of the lesser tubercle" or a "bicipital ridge." Neither of these terms has been generally accepted, nor are they applicable to the Talpidae, indeed "bicipital ridge" is misleading. Therefore I propose to refer to this prominence simply as the "teres tubercle." This tubercle is of no great size in the shrew, but it is rather long (table 11, c). In *Neürotrichus* and *Scapanus*, however, it is separated from the lesser tuberosity as a long, stout ridge on the medial side of the shaft of the humerus. The greater elongation and size in

TABLE 11.—Proportions of the humerus

	a Prox. width no. 1 Length of Humerus	b Prox. width no. 2 Length of Humerus	c Length Teres Tuber. Length of Humerus	d Length Gr. Tuber. Length of Humerus	e Length Less. Tuber. Length of Humerus	f Head Thickness Length of Humerus	g Shaft Width Length of Humerus	h Shaft Thickness Length of Humerus	i Distal Width Length of Humerus	j Length Med. Epic. Length of Humerus	k Length Lat. Epic. Length of Humerus
Sorex	25.9	26.5	36.9	12.6	11.9	20.3	9.4	9.7	33.9	14.3	19.25
Neürotrichus	48.0	51.3	54.0	33.6	19.7	32.3	21.2	18.7	52.9	23.6	22.2
Scapanus	74.0	77.8	62.9	54.0	22.0	42.2	31.9	28.9	70.95	33.4	30.3

the talpines is directly associated with the hypertrophy of the M. teres major and the use of that muscle when the animal is burrowing. Freeman (1886) stated that distinct tubercles are found upon the teres tubercle of *Talpa europaea* for the separate insertions of the Mm. teres major and latissimus dorsi. Since these two muscles fuse and insert together in all talpids so far described, this statement cannot be true.

A distinct widening, enlarging, and distal growth (table 11, a-e) of all proximal processes of the humerus is found to be associated with successive degrees of fossorial life and reflects the greater areas for muscular attachment associated with the more powerful muscles of the more fossorial forms. The more distal extension of these processes also affords a more powerful system of levers for the action of the muscles attaching to them. This subject will be considered further in the section of myology.

The measurement I have termed "head thickness" is more an estimate of the anteroposterior thickness of the proximal part of the shaft of the humerus than an indication of the distance the head projects posteriorly, since the heads of *Neürotrichus* and *Scapanus* do not appear to vary in this particular. Again it is seen (table 11, f) that the more massive humerus belongs to the more fossorial form, which is true no matter which measurement we consider.

In *Sorex* the distal breadth of the humerus is greater than the proximal; in *Neürotrichus* the bone has grown broader at both ends, but the distal end is still slightly larger; in *Scapanus* both ends are greatly expanded, but the proximal is the greater. I cannot think of any particular significance in this slightly greater rate of broadening of the proximal end of the talpine humerus, but with this, as with other slight absolute or relative anatomical differences, the functional differences may be of a nature too delicate to be interpreted.

The great proximal increase of lateral and medial epicondyles is clearly indicated by table 11, j, k. Of these, the medial in *Sorex* is the shorter, but it becomes progressively longer in the talpids. The increase of both epicondyles is

correlated with the proportionate increase in forearm musculature of the fossorial forms.

The distal extension of the proximal processes of the humerus and the proximal extension of the epicondyles, particularly in the talpines, has led to a near approximation of the deltoid process to the lateral epicondyle and of the teres tubercle to the medial epicondyle, with a consequent reduction in the length of the shaft. The shaft has become broadened and thickened in the more fossorial forms (table 11, g, h), a massiveness which is solely an adaptation for greater strength and reflects the stresses put upon the humerus in the everyday life of the shrew, shrew-mole, and mole.

The trochlea and capitulum in *Sorex* (fig. 5E) are generalized and allow horizontal sliding of the humerus on the articular surfaces of radius and ulna. The trochlea and capitulum of *Neürotrichus* and *Scapanus,* however, have undergone radical transformations (fig. 5) and allow little or no lateral and medial shifts. This transformation to achieve a rigidity of the elbow-joint has been accomplished by four major changes: (1) the capitulum, instead of being a mere roller, as in *Sorex,* has assumed the shape of an elongate bulb; (2) the posterior side of the trochlea has gained a high lateral margin; (3) the long axes of the capitulum and, to a lesser extent, of the trochlea have assumed an oblique angle to the long axis of the humerus, whereas in *Sorex* this angle was a right angle; (4) there has occurred a separation of the capitulum and the trochlea by the distal extension of the capitulum; this condition is the opposite of that normal for mammals, since the trochlea usually projects farther distally.

Druzinin (1936) has pointed out that in different mammals different surfaces of the distal end of the humerus make up the trochlea and capitulum. Since these structures may not be homologous throughout a series of mammals, he argues, the names "capitulum" and "trochlea" should be abolished, to be replaced by a new nomenclature which he proposed. However, these old and useful terms can still be used, without any concept of homology, to refer to the distal humeral surfaces used for articulation with ulna and radius, and Druzinin's terms can be employed where exact homology is desirable.

Neither radial nor coronoid fossae are distinct in the shrew, nor is the coronoid fossa distinct in *Scapanus.* The radial fossa in *Neürotrichus* and *Scapanus* is not apparent; in these the capitulum bulges so far anteriorly and distally that no fossa is needed on the humerus to receive the rim of the head of the radius. In marked contrast to *Scapanus,* the coronoid fossa of *Neürotrichus* is deep and merges with the cavity of the supracondyloid foramen. This is not due to the size of the coronoid process of the ulna, which is larger in *Scapanus,* but to the invasion of the fossa by two heads of origin of the M. flexor digitorum sublimus (fig. 31), whereas this muscle arises entirely from the medial epicondyle in *Sorex* and *Scapanus.*

The medial supracondyloid ridge is pierced by the supracondyloid (entepicondylar) foramen in all members of the Soricoidea. Mivart (1867) stated that this is not true of *Sorex murinus;* I question this statement and suspect that he may have found an aberrant individual, as I have, which did not pos-

sess the foramen. Parker and Haswell (1897: 518) stated flatly that the foramen is missing in moles; this error is still present in the most recent edition (1940: 549) of this popular text. The foramen, which is very short in *Sorex*, is converted into a progressively longer tunnel in the more fossorial forms by the proximal extension of the medial epicondyle. As is normal for those mammals possessing it, the foramen transmits the median nerve.

The olecranon fossa becomes progressively deeper in the more fossorial forms. This is not in correlation with the progressively longer olecranon processes in the fossorial genera, as the olecranon is much too long in all ever to be contained in any fossa, but is in correlation with the progressively greater extension of the proximal lip of the semilunar notch in the more fossorial genera (fig. 6). It is only this proximal lip which fits into the olecranon fossa when the forearm is extended; the remainder of the olecranon extends proximally and lies against the posterior musculature of the humerus.

The large pit at the distal end of the medial epicondyle (figs. 5A and 5C) occurs in all members of the Talpidae except *Uropsilus* (Campbell, 1939). It serves as the point of origin for the great ligament of the M. flexor digitorum profundus.

Antebrachium.—The radius and ulna will be considered together, since they are associated so closely as to be a structural unit.

Measurements used: (1) Ulnar shaft length; the distance between the center of the semilunar notch and the center of the distal articular surface of the ulna. This length, rather than the total length of the ulna, was considered valid for comparisons, since the total length includes the length of the olecranon process, which is variable from genus to genus. (2) Olecranon length; the distance between the center of the semilunar notch and the center of the proximal crest of the olecranon. (3) Olecranon breadth; the greatest distance across the proximal crest of the olecranon, measured at right angles to the long axis of the ulna. (4) Distal width of ulna; the greatest distance across the distal articular surface of the ulna, measured at right angles to the long axis. (5) Radial shaft length; the distance from the center of the proximal articular surface to the center of the distal articular surface. (6) Length of the capitular process of the radius; the length of this process was calculated by measuring the total length of the radius and subtracting the length of the shaft. (7) Distal width of the radius; the greatest distance across the distal end of the radius.

TABLE 12.—Relationship between length of shaft of ulna and length of body

	No.	Mean	σ	V
Sorex	13	11.65 ± 0.2	0.7 ± 0.1	6.1 ± 1.2
Neürotrichus	3	12.1 ± 0.04	0.1 ± 0.03	0.5 ± 0.2
Scapanus	8	7.0 ± 0.1	0.4 ± 0.1	5.7 ± 1.4

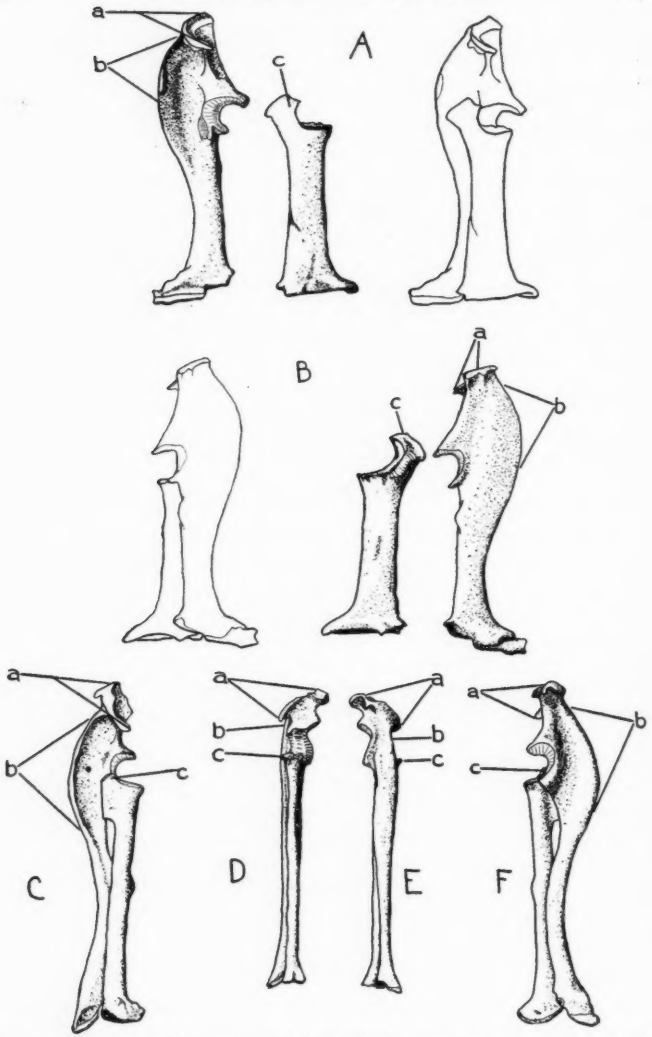

Fig. 6.—A. *Scapanus latimanus*, right ulna and radius, anconeal aspect, ×2.35. B. Palmar aspect of A, ×2.35. C. *Neürotrichus gibbsii*, right ulna and radius, anconeal aspect, ×4.7. D. *Sorex trowbridgii*, right ulna and radius, anterior aspect, ×4.7. E. Posterior aspect of D, ×4.7. F. Palmar aspect of C, ×4.7. a, proximal crest of the olecranon; b, posterior crest of the ulna; c, capitular process of the radius.

TABLE 13.—Relationship between length of shaft of radius and length of body

	No.	Mean	σ	V
Sorex	13	10.6±0.2	0.8±0.2	7.9±1.5
Neürotrichus	6	10.7±0.2	0.4±0.1	3.8±1.1
Scapanus	10	6.7±0.15	0.5±0.1	6.8±0.9

The forearm of every soricoid differs fundamentally from that of man in one important detail: the distal end of the ulna forms a firm hinge-joint with the ulnare of the carpus. Since the radius also forms a hinge-joint with the carpus, pronation and supination, as we know these activities in man, cannot occur for the simple reason that the radius cannot rotate around the ulna, carrying the hand with it. This detail, hitherto unrecognized, is of the utmost importance as limiting the action of the soricoid forearm; any possibility of pronation or supination is further limited in the Talpidae by the capitular process of the radius, a factor mentioned by Slonaker (1920).

The radius and ulna of *Sorex* (fig. 6) are generalized in type. The antebrachium operates in a direct fore-and-aft plane; it is one of a series of levers which all lie and move in this same plane. As such it has no qualities which distinguish it from the antebrachia of other small semi-cursorial mammals; ulna and radius are permanently pronated and the semilunar notch faces forward, with the head of the radius lying below and slightly medial to it. The hand articulates distally so that the palm faces posteriorly and the transverse plane of the hand is continuous with the lateromedial plane of the whole forearm.

Without discussing here the position assumed by the antebrachium with reference to the body, or the relative positions of the hand in correlation with different positions of the antebrachium, it should be pointed out that the radius and ulna of *Neürotrichus* and *Scapanus* have undergone a torsion of their distal ends of such a nature that the radius, instead of crossing the ulna, lies parallel to it. The difference between soricid and talpid conditions is most apparent if one studies the proximal ends of the antebrachia in relation to the long axes of the distal articular surfaces in the three genera (fig. 6). In *Sorex* these long axes, and consequently the transverse plane of the hand, lie in the same plane as does the proximal crest of the olecranon. In *Neürotrichus*, however, the distal ends of the bones have undergone a torsion of nearly 90°, so that the long axes of the distal articular surfaces lie nearly at right angles to the proximal crest of the olecranon.

This torsion is not identical with supination, but the effect upon the hand is the same, therefore I am terming it "pseudosupination."

In *Scapanus* this process of pseudosupination has been carried further, to a full 90°, so that the long axes of the distal ends of the radius and ulna are at right angles to the transverse axis of the proximal crest of the olecranon.

The distal ends of the ulna and radius are so slim in *Sorex* and *Neürotrichus* that the distal articular surfaces lie in line with one another, or nearly so. In *Scapanus*, however, the great thickness of ulna and radius extends

throughout the lengths of their shafts, so that the long axes of the distal articular surfaces, although parallel, lie in different planes. These differences are correlated with comparable differences in configuration of the proximal articular surface of the manus.

The antebrachium of the mole is short, as has been mentioned by Slonaker (1920) and Edwards (1937); this shortening is correlated with an obvious massiveness of the bones, and both shortness and massiveness are correlated with the increased leverage and the increased stresses. The mole has sacrificed speed for strength, with obvious advantages to its mode of life.

The surprising discovery is that *Neürotrichus* has made no progress toward the shortening of the shafts of ulna or radius (tables 12, 13), indeed these bones are as long, or even longer, than are those of *Sorex*. The bones retain, too, an appearance of delicacy, although somewhat less so than those of the shrew. It is obvious that *Neürotrichus* has not sacrificed speed for strength, nor has it acquired a massiveness of structure of forelimb leading to pondercusness of movement. Since *Neürotrichus* is an active animal above ground, hunting for its food and escaping its enemies by running, it can be seen that the relatively long antebrachium is a basic necessity, allowing the animal to run with extreme speed and agility.

The olecranon process in the Soricoidea is distinguished by the possession of a broad "proximal crest" (fig. 6), which serves primarily for the insertion of the M. triceps. The extreme width of the proximal crest in *Scapanus* is correlated with the great size and power of the M. triceps, whereas its intermediate width in *Neürotrichus* and relative narrowness in *Sorex* indicate the diminishing function of this muscle in these genera.

Closely correlated with the width of the proximal process of the olecranon is the length of the olecranon, which is extremely long in *Scapanus*, shorter in *Neürotrichus*, and shortest in *Sorex*. Thus *Scapanus*, with its large M. triceps, long power arm (the olecranon), and relatively short lever arm (the shaft of the ulna), possesses a tremendously powerful lever system for extension of the forearm, an important motion in the talpid type of digging stroke.

The olecranon of *Neürotrichus* is not as long as that of *Scapanus* in relation to the length of the shaft of the ulna, but still it forms a relatively long power arm for extension of the forearm. In *Sorex*, where extension of the forearm is simply a part of the fore limb running stroke, the olecranon is shorter yet.

The semilunar notch is characterized by the growth of the upper border in the more fossorial forms, until in *Scapanus* the articular surface consists of slightly more than half a cylinder, which fits snugly over the trochlea and makes dislocation of the elbow exceedingly difficult. The coronoid process participates to a much less legree in this development of the semilunar notch.

On the surface of the ulna opposite the semilunar notch appears a high ridge, which I am terming the "posterior crest," since it lies on the posterior side of the ulna in *Sorex*, where the primitive relationships of the bone are

maintained. The posterior crest is low in *Sorex*, higher in *Neürotrichus*, and extremely high in *Scapanus*. The posterior crest serves two purposes; it strengthens the ulna at the elbow-joint, a point where great stress develops, and it serves as origins for many of the extensor muscles of the hand and for some of the heads of the M. flexor digitorum profundus. The necessity for an increase of both of these functions, and therefore for an increase in the size and strength of the crest, is greater in the more fossorial forms.

Distally the ulna forms a hinge-joint with the ulnare and pisiform bones, and in *Sorex* the manus is so narrow that the ulna articulates medially with the scapholunar also. In *Sorex* and *Neürotrichus* the articular surface forms an oblique angle with the hand, but in *Scapanus* this is almost a right angle. The articulation is very broad in *Scapanus*, much less so in *Sorex* and *Neürotrichus*, although the latter, in correlation with the larger size of its hand as compared with *Sorex*, has a broader distal articulating surface on the ulna.

The proximal articular rim of the talpid radius has a process not found in other therian mammals; this process (fig. 6c) I am terming the "capitular process" of the radius. It articulates with the posterior surface of the capitulum of the humerus and serves to strengthen the elbow-joint. In *Sorex* the capitular process is scarcely discernible and in *Neürotrichus* extends only a little farther proximally than in *Sorex*. In *Scapanus*, however, the capitular process is almost a fourth as long as the shaft of the radius and converts the proximal articular surface of the radius into a sigmoid cavity which fits snugly over the capitulum. In *Scapanus* the capitular process bears a small facet for articulation with the ulna. The radius of *Neürotrichus* is distinctive in that it has a thin posteriorly directed crest immediately distal to the capitular process.

The shaft of the radius is straight in all forms, but exceedingly massive in *Scapanus*. The distal end is broadened and possesses a groove for articulation with the carpus. The distal breadth is as great as that of the ulna in *Scapanus*, but is less than that of the ulna in the other two genera. The distal breadth of the radius in *Scapanus*, when compared with the length of the shaft, is great and that of *Sorex* relatively small, with the value for *Neürotrichus* lying much closer to *Sorex* than to *Scapanus* (table 14).

The radius articulates with radiale and intermedium in *Scapanus* and *Neürotrichus*, and with the scapholunar (fused radiale, centrale, and intermedium) in *Sorex*.

The surfaces of the ulna and radius are difficult to name in the two talpid genera because of the torsion undergone by the bones. In *Sorex* the surfaces are easily termed lateral and medial, anterior and posterior, according to their natural position, but any one of these surfaces, when considered on a talpid, undergoes a quarter turn from one end of the bone to the other. To evade the issue of homologous surfaces in these circumstances a different terminology must be used. On *Sorex* the term "lateral" and "medial," "anterior" and "posterior" will be used in their normal sense, but for *Neürotrichus* and *Scapanus* the term "anconeal" will designate the view shown in figures 6A and 6C, as though one were looking at the antebrachium with the hand attached, the

"back" or "dorsum" of the hand facing the observer. The opposite view, shown in figures 6B and 6F, will therefore be termed "palmar." Continuing the definitions of the antebrachial surfaces with relation to the hand, the surface toward the pollex will be termed "pollical," the opposite surface "minimal." Thus the semilunar notch is on the anterior face of the ulna of *Sorex*, but on the pollical face of the ulna of a talpid.

Before closing the discussion of the antebrachium it is interesting to note that the radius and ulna in the Soricoidea bear a general resemblance to those of the Monotremata; more particularly the antebrachium of *Neürotrichus* is amazingly similar to that of *Ornithorhynchus*. This resemblance must be attributed to convergence, since *Neürotrichus*, as a talpid, has undoubtedly evolved from a primitive soricid through a type similar to *Uropsilus*, and the antebrachium of a shrew (*Sorex*) bears only a general resemblance to that of a monotreme.

The great resemblance between the forearm of *Neürotrichus* and of *Ornithorhynchus* has undoubtedly occurred by reason of the similarity in stance of the fore leg, with the humerus held laterally and the elbow-joint forming a right angle. With the platypus this stance is possibly basic, inherited from its reptilian ancestors, but with *Neürotrichus* it has been secondarily acquired as a modification for burrowing. In running, the two animals would seem to use the fore limb in exactly the same way (Burrell, 1927, pl. 26). The burrowing methods of the platypus are not so well known as are those of the talpids; in part such motions seem to be similar to those of a mole, but the head and tail are used extensively (Burrell, 1927: 120-124). Burrell (p. 132) speaks of the "scratching" of a platypus while burrowing, but whether this is ventral or lateral scratching is not clear. Nor is it known by actual observation if the platypus ever uses such lateral thrusts of the fore limbs are are characteristic of the mole; certainly the skeletal structure would indicate that the animal is capable of such action, since the coracoid braces the humerus internally in a manner analogous to the clavicular bracing of the humerus of a mole. However, the studies upon the fore limb musculature and the swimming stroke of the platypus by Howell (1937 a, c) would indicate that the animal never employs lateral thrusts of the forearm.

Manus.—Measurements used: (1) Total length; the distance from the center of the proximal articular groove of the carpus to the tip of the claw of the middle finger. The length of the claw was included in this measurement as being a part of the functional length. (2) Hand breadth no. 1; the breadth across the hand at the level of the first phalanges. This excluded the width of the os falciforme in *Scapanus*. (3) Hand breadth no. 2; the same as hand breadth no. 1, but including the width of the os falciforme. The measurement can be made on talpines only. (4) Carpal length; the distance from the midpoint of the proximal articular surface of the intermedium to the midpoint of the distal articular surface of carpale III. (5) Length of metacarpal III. (6) Length of claw III. (7) Length of finger III; the distance from the middle of the proximal articular surface of metacarpal III to the distal tip of claw III.

TABLE 14.—Proportions of the antebrachial elements

	Olecranon Length / Ulnar Shaft Length	Olecranon Breadth / Ulnar Shaft Length	Distal Ulnar Breadth / Ulnar Shaft Length	Capitular Process / Radial Shaft Length	Distal Radial Breadth / Radial Shaft Length
Sorex	18.9	19.3	13.9	1.5	11.5
Neürotrichus	26.9	33.9	17.7	6.0	20.4
Scapanus	64.2	55.9	52.4	23.3	55.1

TABLE 15.—Relationship between length of manus and length of body

	No.	Mean	σ	V
Sorex	11	11.4 $\pm$0.2	0.8$\pm$0.2	6.7$\pm$1.4
Neürotrichus	3	13.05$\pm$0.4	0.7$\pm$0.3	5.0$\pm$2.05
Scapanus	2	12.1 $\pm$0.1	0.1$\pm$0.05	0.8$\pm$0.2

The small number of skeletons of *Neürotrichus* and *Scapanus* for which body lengths and hand lengths could both be procured necessitated another type of approach to the problem of their relative lengths. Therefore all the body lengths and all the hand lengths for each genus were averaged, irrespective of the skeletons to which they belonged, and a percentage taken from these means. This procedure resulted in a proportion of body length to hand length of 12.5 per cent of *Neürotrichus* and of 13.5 per cent for *Scapanus*. Thus the true value for neither genus can be determined on the basis of existing data, but it lies somewhere between 12.1 per cent and 13.5 per cent.

Although it cannot be stated whether the manus of *Scapanus* or of *Neürotrichus* is longer, both are slightly longer than is that of *Sorex*. This additional length is due to the great length of claw in the talpids (table 16); without the claws the talpid hands would undoubtedly be relatively shorter than are the soricine hands.

Although highly specialized for digging, the talpid hand is of a primitive pattern, since only carpales IV and V are fused, forming a hamatum (unciform), and both intermedium and centrale are retained as separate bones; Owen (1866: 392) misnamed the centrale as the intermedium and Edwards (1937) incorrectly synonymized the two terms and applied them to the centrale. In *Sorex* the centrale and intermedium are not separate but are fused with the radiale to form a scapholunar. In this respect the talpids are more primitive than are the soricines.

The talpine hand is noted for its possession of the large os falciforme (radial sesamoid), a sickle-shaped bone lying on the medial (pollex) surface of carpus

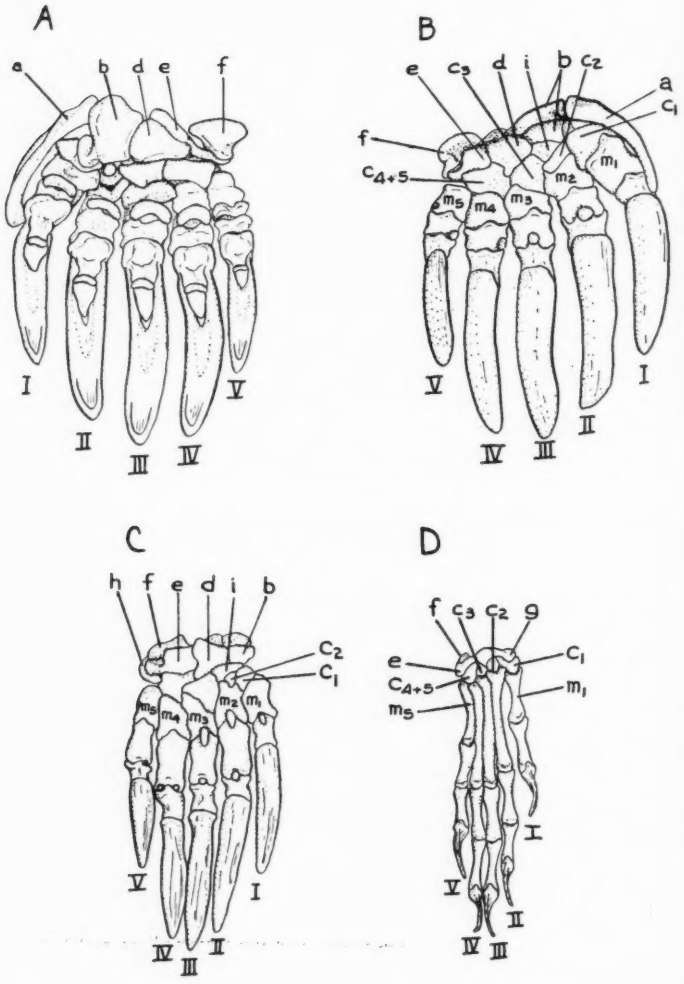

Fig. 7.—A. *Scapanus latimanus*, right manus, palmar aspect, ×2.5. B. Dorsal aspect of A, ×2.5. C. *Neurotrichus gibbsii*, right manus, dorsal aspect, ×5. D. *Sorex trowbridgii*, right manus, dorsal aspect, ×5. a, os falciforme; b, radiale; c, carpale; d, intermedium; e, ulnare; f, pisiform; g, scapholunar (radiale+intermedium+centrale); h, ulnar sesamoid; i, centrale; m, metacarpal.

and metacarpus. Proximally this bone touches the radiale, but has no true joint with it. Lying between the falciform and the radiale, on the dorsal surface, is another small sesamoid, hitherto unnoted and probably unimportant. What is considered by the writer to be the homologue of the falciform bone is found in *Neürotrichus* as a small, flat sesamoid which lies on the mediopalmar aspect of the radiale and is contained within the medial tendon of the M. palmaris longus. This tendon in *Scapanus* inserts on the falciform bone. *Sorex* has no homologue of this sesamoid, nor does it have a tendon of the M. palmaris longus to the medial side of the hand. No radial sesamoid has been noted in *Uropsilus* (A. Milne-Edwards, 1868-1874: 276), in *Desmana* (Dobson, 1883: 147), or in *Urotrichus* or *Galemys* (Mivart, 1868), but such a small bone might easily be lost or overlooked.

The os falciforme of the Talpids was termed "praepollex" by von Bardeleben, (1894), but he used this term (as he did also "praehallux" and "postminimus") in a positional sense, without reference to evolutionary theory or supposed homology. The use of such terms in this sense is confusing, however, as they do generally indicate a meaning of homology, and, in my opinion, should be so limited.

The presence or absence of a falciform bone cannot be used as a character by which to distinguish the Desmaninae from the Talpinae, but the relative size of the bone must be considered as one of the criteria. In this respect *Condylura* (Dobson, 1883, pl. 19, fig. 3a) occupies an intermediate position between the two subfamilies, as it does in so many other characters.

Neürotrichus has a sesamoid capping the lateral tip of the ulnare; this small sesamoid is not found in the other two genera investigated. In *Neürotrichus* this sesamoid has developed within the tendon of the M. extensor carpi ulnaris where the tendon crosses the ulnare, but in *Sorex*, where the hand is much narrower, there presumably has been no need for such a sesamoid. In *Scapanus* the insertion of this muscle has shifted from metacarpal V to digit IV, and consequently does not cross the lateral corner of the ulnare, so that no sesamoid is present.

I am at a loss to explain the statement by Godman (1826: 106) that the hand of *Scalopus* possesses a "cartilaginous additament" lateral to the fifth finger, comparable to the os falciforme of the pollex; *Condylura* did not have this "additament," he said, and thus the hand of the star-nosed mole was narrower than was that of *Scalopus*. I have found no other statement as to the presence of such a structure in any talpid, nod did I find it in either *Scapanus* or *Neürotrichus*.

The remaining sesamoids of the hand, although numerous, do not deserve special comment; they can be observed in figure 7.

The more fossorial talpids possesses the larger claws, and in all (with the possible exception of *Uropsilus*) they are larger than in the Soricidae. The soricine claw is high dorsopalmarly, but the talpid claw has formed a spadelike surface and become flattened, except in *Uropsilus*, where it is of the soricine

type (A. Milne-Edwards, 1868-1874: 276; Allen, 1938: 55; Winge, 1941: 172).

The claw of *Sorex* is a dorsal covering to the distal phalanx, but in *Talpa, Mogera, Scalopus, Scapanus, Parascalops, Condylura, Neürotrichus,* and *Urotrichus* (all examined by the writer) the margins of the claw have encroached upon the ventral surface until they have met and fused, forming a hollow sheath.

The Talpidae have sometimes been defined as having the distal phalanx of the manus dorsally grooved and distally bifurcated for the reception of the claw. Of the genera investigated by me, this is true for *Talpa, Mogera, Scalopus, Scapanus, Parascalops,* and *Condylura* (Dobson's statement, 1883: 164, that the claws of *Condylura* are not bifid or grooved is incorrect), but less true for *Neürotrichus* and *Urotrichus,* where the groove is shallower and the distal tips of the phalanges may be bifid, square, or jagged. The distal phalanges of *Uropsilus* are not bifid (A. Milne-Edwards, 1868-1874: 276), nor do the shrews have any such modification. The grooved and bifid phalanx is an obvious adaptation for strengthening the union of phalanx and claw, and the distribution of this modification within the Talpidae is in correlation with the fossorial activities of the genera.

In *Sorex* the distal phalanx extends nearly to the end of the claw, but in all the talpid genera available to me it does not extend over three-fourths of the distance; the claw alone has become strong enough to withstand the stress involved in the digging stroke.

The hands of *Talpa, Mogera, Scalopus, Scapanus,* and *Parascalops* are webbed to the end of the second phalanx; those of *Condylura, Urotrichus,* and *Neürotrichus* are not, but *Condylura* has the phalangeal pads expanded laterally to form flattened cones between the toes, and this device partially serves the same purpose as webbing. This development of the phalangeal pads of *Condylura* was first noted by Godman (1826: 104).

The dorsopalmar thickness of the bones of the manus was not measured, but is noticeably greatest in *Scaapnus,* intermediate in *Neürotrichus,* and least in *Sorex;* these differences are correlated with the obvious needs of the three genera as to strength of manus. The great thickness of the manus in *Scapanus* allows the articulation of the radius and ulna to occur in different planes, which is necessary due to the great thickness of those bones.

The proportions of the hand of *Sorex* are typical for a small semicursorial mammal, and in this it is primitive. The evolutionary tendencies within the hands of the Talpidae are clear from table 16: there has been a broadening of every element of the hand, a great lengthening of the claws and the distal phalanges, a lesser lengthening of the carpus, and proportional shortening of the metacarpals and the first and second phalanges of each digit. No talpid hand, however, has widened enough to excavate the full width of the burrow with one stroke, as claimed for *Condylura* by Shimer (1903).

The process of elongation of the carpal bones is almost finished by the

neürotrichine stage of evolution, but the lengthening of the distal phalanges and shortening of the metacarpals and other phalanges has proceeded further, to the condition found in *Scapanus;* this process may not have yet reached an equilibrium in the talpines. The exact manner and rates at which these changes occurred cannot be determined until we know more of the phylogeny of the talpid genera.

TABLE 16.—Proportions of the manus

	Hand Breadth no. 1 / Hand Length	Hand Breadth no. 2 / Hand Length	Carpal Length / Hand Length	Length Metacarp. III / Hand Length	Length Claw III / Hand Length	Length Finger III / Hand Length
Sorex	25.3	—	9.5	36.55	24.0	90.5
Neürotrichus	43.7	—	16.85	18.25	45.0	82.7
Scapanus	76.0	79.1	17.8	11.4	55.9	82.4

The differential growth rates for different parts of the hands of the three genera has resulted in the manus of *Scapanus* and of *Neürotrichus* being of approximately equal relative lengths and each but little longer than that of *Sorex* (table 15), yet the proportion of parts within each hand is radically different (table 16; fig. 7). The question that presents itself is: What is the advantage to the animal from this proportion of parts?

So long as the hand stays approximately the same relative length, as it has in these soricoids, it is obvious that the elongation of the claws, irrespective of what happens in the remainder of the manus, can produce but one result. The insertions of the long flexor and extensor muscles will be moved proximally, away from the distal end of the manus where the work of the muscles is accomplished.

A proximal insertion into a long claw can only mean that the more fossorial forms have greater speed of flexion and extension of the claws, and incidentally of the phalanges, with a simultaneous loss of power. Such a loss of power can be understood in the act of extension, which is merely a recovery stroke where power is not so essential and speed may be desirous.

The sacrifice of power for speed in the act of flexion appears to be a dilemma until one understands the action of the M. flexor digitorum profundus; this latter consists of but a few small muscular heads and one great ligamentous band which runs between the medial epicondyle of the humerus and the distal phalanges of the manus. This ligament is the principal flexor of the digits and acts when the medial edge of the humerus is rotated posteriorly by the Mm. teres major, latissimus dorsi, subscapularis, and pectoralis superficialis posticus. (The action of these muscles in this manner is explained in full in the section on myology, p. 655). Thus the mole is actually using the most powerful

muscles of its shoulder in the act of flexing its digits, and can afford to sacrifice some of that tremendous power for speed, since in this way the animal still has all the power it can possibly use for flexion and has also gained speed of action. If the animal has the strength to use long claws, it is obvious that they are more advantageous than are short ones, since the claws are the agents which actually loosen the soil.

One might imagine that, as the claws had become lengthened in the talpids, all the other elements of the hand would have shortenede proportionally, but this is not true inasmuch as the carpus has also lengthened. What function this lengthened carpus serves in the fossorial genera is not understood.

SUMMARY OF THE SKELETON OF THE FORE LIMB

For calculations concerning the fore limb as a whole, the length of arm has been defined as the length of the humerus plus the length of the ulnar shaft plus the length of the manus.

TABLE 17.—Relationship between length of arm and length of body

	No.	Mean	σ	V
Sorex	13	32.4±0.7	2.6± 0.5	8.0±1.5
Neürotrichus	3	33.7	32.7—35.0	
Scapanus	1	28.8	(extremes)	

The figures for *Neürotrichus* and *Scapanus* in table 17 are inconclusive due to the small series, but no other data are available for *Neürotrichus*. For *Scapanus*, if the data are gathered for all the arm lengths and all the body lengths available, irrespective of the fact that these measurements came from different animals, one obtains a relationship of length of arm to length of body of 30.2 per cent, which is still lower than any of the values for *Sorex* or *Neürotrichus*.

One would expect the arm of *Scaapnus* to be somewhat shorter, relatively, than are those of *Sorex* or *Neürotrichus*, since the ulnar shaft of *Scapanus* is relatively so short, while humerus and hand do not differ so much from those of the two genera.

The relationship between the length of each bone of the fore limb and the length of the body has been set forth in the previous tables, and the relative lengths of the bones in the different genera have been discussed as to their bearing upon the locomotion of those genera. One may now continue with an analysis of the relationship between individual bones of the fore limb and the total length of the fore limb. Information derived from this type of calculation is of value when used to indicate the relative length of any one lever arm as compared with others within the same series, so that the mechanical advantages of one such system may be compared with those of another. The limita-

tions of this type of information, however, must be recognized; it cannot, for instance, be used to compare directly the lengths of two humeri of different genera and from such comparison to claim that one humerus is the longer. One humerus may be relatively longer than another within an arm, as the mole's is longer than the shrew's (table 18), but when compared to body length (table 10), it is found that the humerus of the mole has not elongated, but that the ulnar shaft has shortened (table 12). Actually, in this type of calculation, one is comparing one variable (the length of one bone) with the sum of several variables (the lengths of all the bones of a limb), and must be careful as to the type of conclusions derived from such information.

TABLE 18.—Relationship between length of humerus and length of arm

	No.	Mean	σ	V
Sorex	22	32.1±0.2	0.8±0.1	2.5 ±0.4
Neürotrichus	6	29.1±0.3	0.7±0.2	2.55±0.7
Scapanus	12	35.8±0.1	0.5±0.1	1.3 ±0.3

TABLE 19.—Relationship between length of shaft of ulna and length of arm

	No.	Mean	σ	V
Sorex	22	35.8±0.2	1.0±0.15	2.8±0.4
Neürotrichus	6	33.6±0.6	1.4±0.4	4.3±1.2
Scapanus	12	23.5±0.3	0.9±0.2	4.0±0.8

TABLE 20.—Relationship between length of shaft of radius and length of arm

	No.	Mean	σ	V
Sorex	22	32.8±0.2	0.8±0.1	2.55±0.4
Neürotrichus	6	31.1±0.6	1.4±0.4	5.4 ±1.6
Scapanus	12	22.3±0.2	0.6±0.1	2.6 ±0.5

TABLE 21.—Relationship between length of manus and length of arm

	No.	Mean	σ	V
Sorex	22	35.1±0.3	1.2±0.2	3.5±0.5
Neürotrichus	6	37.5±0.5	1.3±0.4	3.4±1.0
Scapanus	12	41.9±0.3	1.0±0.2	2.4±0.5

To understand any discussion of the movements of the bones in the action of the soricoid fore limb it must be remembered that the soricid and the talpid limbs function on entirely different plans. The soricid type is simple and requires no further analysis, but an overall review of the osteology of the talpid fore limb is necessary for a complete understanding of its actions.

The talpid type of burrowing is restricted to three fundamntal strokes: (1) "breast-stroke," used only in very loose earth; (2) the raising of the roof of a shallow burrow by simultaneous lateral extension of all elements of both fore limbs; (3) a forward extension of the arm, followed immediately by a lateral scratching stroke in deep burrows, where the earth is hard. Actually, each of these strokes is fundamentally the same, inasmuch as each consists of an anterior extension of the arm, followed by more or less of a lateral sweep. The fore limb of *Neürotrichus* is capable of another motion, since it can be brought beneath the body with the palm upon the ground.

In review, the following paragraphs concern essential points in the osteology of the talpid fore limb:

1. The pectoral girdle has moved anteriorly beneath the head, due to the lengthening of the manubrium. The deepening of the manubrium has given greater surface for the origin of certain pectoral muscles.

2. In *Scapanus* the joint between clavicle and manubrium is predominantly a hinge-joint allowing only anteroposterior movement; also the clavicle is extremely short. Thus the proximal end of the humerus can undergo no dorsoventral change in position, nor can the head of the scapula; for this reason the elevator muscle for the shoulder-joint (M. trapezius anticus) has degenerated. In *Neürotrichus* the joint between clavicle and manubrium is not so definitely a hinge-joint and the clavicle is longer. Thus a change in position of the shoulder-joint is allowed, and the M. trapezius anticus has not disappeared (fig. 26).

3. The talpid scapula has changed from the primitive soricine position to one in which it points anteroventrally. It has increased its length, decreased the height of the spine, and the axillary border has encroached dorsally upon the infraspinatus fossa, which is progressively degenerate in the more fossorial forms. The glenoid fossa has become elliptical.

4. The greater tuberosity of the humerus abuts upon, and has a joint with, the distal end of the clavicle. This joint is of a shallow ball and socket type.

5. The head of the humerus has retreated to the posterior side of the shaft and becomes elliptical to fit into the elliptical concavity of the glenoid fossa of the scapula. The angle of the head of the humerus with the shaft of the humerus determines the angle at which the humerus projects from the body; the resultant position is fundamentally lateral in *Neürotrichus* and dorsolateral in *Scapanus*.

6. The raising and lowering of the distal end of the humerus (abduction and adduction) must be accompanied by rotation of the scapula, due to the nature of the humeroscapular joint.

7. The nature of the humeroscapular joint does not preclude rotation of the humerus on its own long axis; the long axes of the head and of glenoid fossa are still parallel. The increased breadth of the proximal part of the

humerus affords the muscles performing this rotation a greater leverage in *Scapanus* than in *Neürotrichus*.

8. The elbow is a hinge-joint, allowing only extension and flexion of the forearm.

9. The decreased length of shafts of ulna and radius and the increased length of olecranon allows *Scapanus* a greater mechanical advantage in extension of the forearm than has *Neürotrichus*.

10. No supination or pronation is possible in any soricoid antebrachium.

11. If a fore limb of the soricine type is imagined to be held in the standing position of *Neürotrichus*, with the humerus held laterally and the antebrachium half-flexed, then the forearm would extend anteriorly and the manus would touch the ground upon the medial side of the thumb only, with the palm facing laterally. But the shafts of ulna and radius of *Neürotrichus* have undergone nearly 90° of torsion, which brings the hand around so that the palm can rest flat upon the ground.

12. If from the position with its palm upon the ground *Neürotrichus* were to extend the forearm completely (an action which probably never happens singly), the arm would be extended laterally, with the palm down. If the humerus is now rotated so that its true medial surface faces posteriorly, the antebrachium and the hand will turn with it, so that the palm of the hand turns posteriorly. This is the position of the arm and manus in the digging stroke, but is accomplished by rotation of the humerus before or simultaneously with the extension of the forearm, and is accompanied by partial flexion of the hand and phalanges.

13. Rotation of the humerus by the shoulder muscles automatically flexes the digits and the hand, which action is part of the digging stroke.

14. If the humerus of *Neürotrichus* were to extend dorsolaterally or almost dorsally, the palm could not be placed upon the ground in any position, but would face lateroventrally or laterally with the forearm half-flexed, and only the medial side of the thumb would rest upon the ground. This is the condition in *Scapanus*, and thus in the true mole, when the humerus is rotated so that the true medial side faces posteriorly, the palm of the hand is turned dorsolaterally, although it is not turned so far as it would be if *Neürotrichus* were actually to assume this position, because the pseudosupination of the shafts of ulna and radius has progressed to a full 90° in *Scapanus*.

15. The talpid wrist-joint is a hinge joint, allowing only flexion and extension of the manus.

16. The manus of *Scapanus* has developed into a more useful digging tool than has that of *Neürotrichus*, inasmuch as it is wider, thicker, has an os falciforme, and the claws are wider, longer, and stronger. In both genera the manus is automatiaclly flexed by rotation of the true medial side of the humerus posteriorly.

17. Except for the angle which the humerus makes with the body, the relative differences in the lengths of some of the bones, and the differences in proportion of the parts of individual bones, the fore limbs of *Scapanus* and *Neürotrichus* are basically alike; the digging stroke is fundamentally similar.

THE HIND LIMB

Sacrum.—The sacrum consists of five vertebrae in *Sorex, Neürotrichus, Scapanus,* and *Scalopus,* although in *Sorex* the posterior two are poorly fused and approach caudal vertebrae in type. In the single example of *Crocidura russula* available to me there are four sacral vertebrae firmly fused together and one posterior vertebra which could be considered either sacral or caudal. Leche (1883: 15) has discussed the sacra of other soricoids. Presumably all talpids have five sacral vertebrae, although figure 80 of Puisségur's paper (1935) would indicate six for *Galemys;* Leche (1883: 13-15) reported five present in *Talpa, Mogera, Condylura, Urotrichus,* and *"Myogale."* Chapman (1919) considered the soricoid sacrum to consist of three sacral vertebrae, to which caudal vertebrae may fuse.

The length of the sacrum, as measured along the centra (table 22) does not seem to bear any relation to the modes of life of shrew, shrew-mole, and mole, as the length is relatively the same in each genus; one cannot assign any importance for the possible slight shortening in *Scapanus.*

There is, however, a positive correlation in two characters between the mode of life and the morphology of the sacrum: (1) the sacral vertebrae are most firmly ankylosed in *Scapanus* and only slightly less so in *Neürotrichus,* but in *Sorex* the anterior three vertebrae are united while in the posterior two the fusion has not been carried to completion, although they are more firmly united than are caudal vertebrae; (2) the dorsal tips of the spinous processes of the anterior three or four sacral vertebrae are fused in *Sorex,* all five sacral vertebrae are so united in *Neürotrichus,* and in *Scapanus* the five sacral spinous processes are united into a solid ridge which runs the length of the sacrum (fig. 8).

TABLE 22.—Relationship between length of sacrum and length of body

	No.	Mean	σ	V
Sorex	13	14.7 ±0.3	1.1±0.2	7.4±1.5
Neürotrichus	10	14.9 ±0.2	0.8±0.2	5.1±1.1
Scapanus	21	14.25±0.2	0.8±0.1	5.6±0.9

These two modifications make the talpid sacrum a strong, united unit, whereas the soricine sacrum is much less so. Within the talpids, the sacrum of *Scapanus* is stronger than that of *Neürotrichus.* There is, then, a direct correlation between a stronger sacrum and the more fossorial type of life; this correlation is merely a part of the pattern of adaptation to the fossorial life of

the talpid hind limb and is related directly to the greater thrust received from the hind limb of the more fossorial animals.

Pelvic girdle.—Measurements: (1) Length of innominate; the distance from the anterior tip of the iliac crest to the posterior tip of the pubis, measured parallel with the long axis of the body. (2) Interpubic distance no. 1; an inside measurement, from medial surface to medial surface at the closest approximation of the pubic bones, taken at the anterior end of the pubic bones and directly posterior to the iliopectineal process. (3) Interpubic distance no. 2; an outside measurement, from lateral surface to lateral surface, taken across the descending rami of the pubic bones. (4) Height of innominate; the dorsoventral distance from the dorsum of the innominate to the ventrum of the pubis, at the level of the acetabulum. (5) Interacetabular distance; from the shallowest point on the rim of one acetabulum to the same point on the other acetabulum. (6) Lumboacetabular distance; from the anterior edge of the acetabulum to the anterior end of the first sacral centrum, measured parallel with the long axis of the sacrum. (7) Interiliac distance; an outside measurement, from lateral surface to lateral surface, of the greatest distance across the iliac crests.

The lengths of ilia, ischia, and pubes could not be measured, since the exact boundaries of these bones cannot be determined on adult skeletons.

TABLE 23.—Relationship between length of innominate and length of body

	No.	Mean	σ	V
Sorex	13	16.05 ± 0.4	1.45 ± 0.2	9.05 ± 0.8
Neürotrichus	7	20.1 ± 0.3	0.7 ± 0.2	3.6 ± 0.6
Scapanus	22	18.4 ± 0.2	1.0 ± 0.15	5.45 ± 0.9

The long axis of the soricoid innominate is parellel, or nearly so, with the long axis of the sacrum. This condition is a highly specialized one for mammals, most of which deviate to a lesser degree from the ancestral type of pelvis of the therapsid reptiles, in which the ilium is transverse to the sacrum, the pubis anterior and below the ilium, and the ischium posterior and below the ilium. Although the ilium, even in some primitive mammals as *Echidna* and *Didelphis*, may tend to become parallel with the sacrum, the pubis and ischium in most mammals project ventrally or posteroventrally to form a symphysis. The soricoid pubis and ischium, however, project posteriorly from the ilium (fig. 8). This condition is in no sense "bird-like," since the ilium does not project posteriorly beyond the acetabulum.

I think it is obvious that the nearer the innominate is parallel with the sacrum the more advantageously power can be transmitted to the sacrum from the innominate without loss due to dorsally directed end-thrust; but this is a principle as useful to cursorial as to fossorial forms. Also, as the acetabulum becomes placed higher in relation to the sacrum, the total effect is a depression

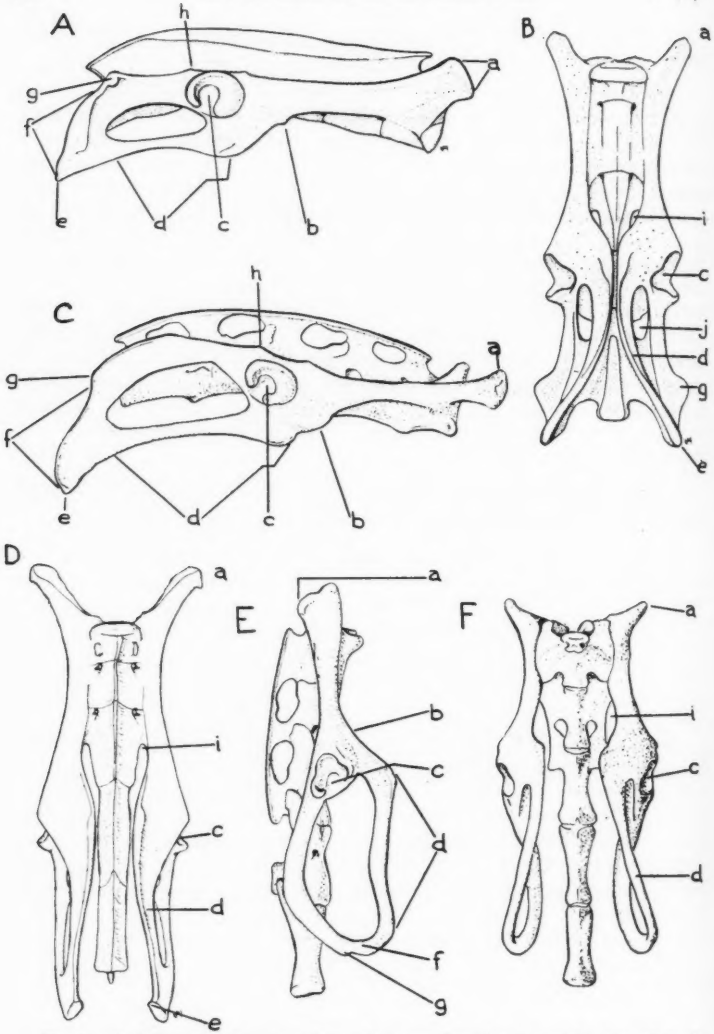

Fig. 8.—*A. Scapanus latimanus,* pelvis and sacrum, lateral aspect, right side, ×2.5. B. Ventral aspect of A, ×2.5. C. *Neürotrichus gibbsii,* pelvis and sacrum, lateral aspect, right side, ×5. D. Ventral aspect of C, ×5. E. *Sorex trowbridgii,* pelvis and sacrum, lateral aspect, right side, ×5. F. Ventral aspect of E, ×5. a, crest of the ilium; b, iliopectineal process; c, acetabulum; d, horizontal ramus of the pubis; e, spine of the pubis; f, descending ramus of the pubis; g, tuberosity of the ischium; h, spine of the ischium; i, greater sciatic notch or foramen; j, lesser sciatic foramen.

of the rear of the animal; in a fossorial animal this is of great importance since it allows free movement of the hind limbs in a low-roofed tunnel.

As the pubis becomes directed more posteriorly and less ventrally, the pubic symphysis approaches the sacrum more closely. The pelvic orifice is thus restricted and, if the condition were to prevail, survival of the species would be threatened due to the loss of females and young during parturition. The geomyid rodents evade this possibility by resorption of the pubic symphysis in the sexually mature female (Hisaw, 1924, 1925); the male retains the symphysis. All Soricoidea, except *Desmana* and *Galemys*, lose the symphysis entirely in both sexes, and Puisségur (1935) stated that the female *Galemys* also loses the central part of the symphysis. Even so, said Puisségur, the pelvic outlet in the female *Galemys* is more restricted than in *Talpa*, and for this reason the litters of the former are smaller.

Thus the soricoid pubic symphysis presents a very interesting situation. The common statement that the moles and shrews have no pubic symphysis and that the urogenital and intestinal tracts pass ventral to the pelvic cavity in the Talpinae are both false, as has been noted also by Lyon (1936: 28).

Embryonically a talpid pubic symphysis of a normal mammalian type is laid down in cartilage between the descending pubic rami; the intestinal and urogenital tracts pass through this pelvic orifice in the normal manner. Such an embryonic symphysis has been described in *Talpa* (Leche, 1880; 1883, fig. 31), in *Scalopus* (Hisaw and Zilley, 1927), and in *Parascalops* (Eadie, 1945). In embryos of shrews (*Crossopus fodiens*, *Crocidura murina*) Leche (1883: 18) found only a ligamentous band connecting the two pubes.

In *Galemys* and *Desmana* the pubic symphysis is retained in the adult (Brandt, 1836; Leche, 1883, figs. 22, 25; Dobson, 1883, pls. 15, 17; Puisségur, 1935, figs. 80, 83). Brandt thought this connection lay between the ischia; he stated that it may be cartilaginous or bony. Dobson regarded the connection more as an interpubic ligament, but stated that it is ossified. In no other soricoid investigated to date has any remnant of the true pubic symphysis been found in the adult, although Hisaw and Zilley (1927) found a ligamentous band with similar morphological relationships in the half-grown *Scalopus*, and Jacobson, 1842 (quoted by Leche, 1883: 18) seemingly described the same thing in an adult *Talpa europaea*.

In *Neürotrichus* there is a definite tendinous band which crosses between the tips of the descending rami of the pubes, ventrally to the urogenital and intestinal tracts. From this band originate many of the fibers of the decussating Mm. recti abdomini. Transitional stages between the cartilaginous pubic symphysis of the embryo and the tendinous band of the adult have not been described.

In a mole, *Scapanus townsendi*, by dissecting carefully at the posterior edge of the decussating Mm. recti abdomini, there were found a few tendinous fibers

which crossed between the tips of the descending rami of the pubes. It might be argued that any muscles which arise from two adjacent points and then cross, as do the Mm. recti abdomini, would have fibrous connective tissue to strengthen the point of crossing, but in shrews (*Sorex palustris, S. trowbridgii,* and *Blarina brevicauda* were dissected) such is not the case; the muscles cross cleanly without a trace of connective tissue between the pubes. I can only conclude that all trace of the embryonic pubic symphysis has been lost in the Soricinae.

The increased length of the innominate of *Scapanus* over that of *Sorex* and of *Neürotrichus* over that of *Scapanus* (table 23), is due in part to the increase in length of the descending ramus of the pubis. No particular correlation with mode of life or muscular attachments is believed to account for this difference in osseous structure, but rather the greater tendency for the Desmaninae to form a pubic symphysis, of which the descending ramus of the pubis is a remnant; this tendency would generally seem to be more manifest in the Talpidae than in the Soricidae.

In part the differences in lengths of innominates can be attributed to the more posterior displacement of the acetabulum of *Scapanus* as compared with *Neürotrichus* and of *Neürotrichus* as compared with *Sorex* (table 24). This posterior displacement of the acetabulum is, in effect, a measure of increased length of ilium. In agreement with this, Puisségur (1935) noted the increased length of the ilium of *Talpa* as compared with *Galemys*. The relationship between an increased length of ilium and the fossorial life is not clear; perhaps the increased length of ilium that can be ankylosed to the sacrum is an advantage to a fossorial mammal which must transmit the powerful thrusts from the hind legs through the sacro-iliac junction.

Ossification of the soricid innominate has never been investigated, and that of the talpid innominate only by Leche (1883, figs. 21, 29) in *Galemys* and *Talpa*. In these genera the acetabulum is formed entirely from the acetabular bone and the ischium; the pubis and ilium are excluded from the acetabulum. The iliopectineal process lies wholly on the ilium, but the narrowest point between the two innominates (the point of pseudosymphysis) lies wholly on the pubis. The ventral and posterior borders of the obturator foramen are derived from the horizontal and descending rami of the pubis, respectively; the ischium is merely a dorsal bar to the obturator foramen and terminates posteriorly immediately behind the tuberosity of the ischium. The attempt by Slonaker (1920, figs. 4-6) to determine the limits of these bones on adult skeletons led him into complete error if Leche is correct; it is curious that Slonaker did not quote Leche's paper in his extensive bibliography.

The attachment of the innominates to the sacrum is of great importance in the Soricoidea. In *Sorex* the sacro-iliac joint is an amphiarthrosis, similar in type to that found in man but of a looser nature, so that in prepared skeletons the bones often fall apart. The joint lies between the anterior part of the ilium

and the first and sometimes a small part of the second sacral vertebrae; actually, it is as weak a sacro-iliac joint as can be found in any but aquatic mammals.

In *Neürotrichus* the sacro-iliac joint lies between the ilium and the first three sacral vertebrae; the extent of the participation of the third vertebra shows extreme individual variation and may vary on the two sides of the same animal. Ilium and sacrum have ankylosed completely so that often the suture cannot be found; an attempt to separate the bones at the joint will often result in a broken ilium.

The situation in *Condylura* (Chapman, 1919) is comparable to that in *Neürotrichus*, but in *Scapanus* and the remaining members of the Talpinae the ilium and ischium are ankylosed to all five sacral vertebrae. The extent of the participation of the ilium is no more than in *Neürotrichus;* the added connections are two bony bridges between the ischium and the posterior two sacral vertebrae. According to the studies of Leche (1883: 19) on young individuals of *Talpa europaea, T. coeca, Mogera wogura, Parascalops breweri,* and *Condylura cristata,* the two bony bridges are formed by the ossification of a posterior tuberoso-sacral ligament, between the tuberosity of the ischium and the transverse process of the "fourth sacral vertebra" (his figures, however, show it attaching to the fifth, as it should), and an anterior spinoso-sacral ligament, between the spine of the ischium and the fourth sacral vertebra (Leche does not specify which vertebra). The greater sciatic foramen would thus lie between the true sacro-iliac joint and the anterior bridge; the lesser sciatic foramen would lie between the anterior and posterior bridges.

Mysberg (1917) investigated this problem more completely. He agreed with Leche that the anterior bridge is the spino-sacral ligament, but, on the basis of the course of a branch of the pudendal nerve, he found that the posterior bridge is the ossified iliococcygeal ligament, which in turn represents a ligamentous portion of a primitively more extensive M. iliococcygeus.

In the genera studied to date there is complete correlation between the degree of ankylosis of the innominate to the sacrum and the degree of fossorial life. This stronger support in the more fossorial animals indicates a proportionately greater thrust from the hind limbs, a thrust which is not precisely in the direction of the long axis of the body. A thrust in the direction of the long axis of the body would transmit no mediolateral torque to the innominate, only anterioposterior; as this anteriorposterior torque is increased with increase in power, a lengthened ankylosis between sacrum and ilium would probably compensate for any possible increase in power of which the talpid hind limb is capable.

As soon, however, as the limb is placed laterally and power applied, a mediolateral component is added to the strain on the innominate and is transmitted through the acetabulum, a point which lies behind the sacro-iliac joint and thus a point not supported medially. The ligaments between the sacrum and the ischium prevent the ischium from breaking away, but there is little to

keep the ischium from collapsing inward under pressure unless these ligaments ossify, and in the more fossorial talpids they have done so.

Those talpids which burrow deeply and bring dirt to the surface to form mole-hills have the ankylosis between the ischium and sacrum, and it is this strenuous part of their locomotor activity, in my opinion, which must be considered responsible for that union. Moles run through their burrows straddling the bottom, and thus with the legs held semilaterally; presumably they assume the same pose when pushing dirt through the burrow. As usual, *Condylura* is an exception, inasmuch as it has no ossification between sacrum and ischium, but nevertheless it does make mole-hills under some circumstances (Seton, 1909: 1142), but students of *Condylura* agree that it seeks out the softer soils adjoining water courses, where the earth is softer and more easily tunneled, so that mole-hills are not so necessary.

TABLE 24.—Proportions of pelvis

	Interpubic Dist. no. 1 / Length of Sacrum	Interpubic Dist. no. 2 / Length of Sacrum	Height of Innominate / Length of innominate	Height of Innominate / Length of Sacrum	Inter-acetabular Dist. / Length of Sacrum	Acetabular Distance / Length of Sacrum	Inter-iliac Distance / Length of Sacrum
Sorex	18.5	42.8	20.9	22.5	44.1	35.0	38.2
Neürotrichus	13.3	33.6	19.2	24.9	32.5	47.3	46.9
Scapanus	2.2	42.05	18.2	23.4	29.2	52.7	41.5

In all members of the Talpinae there is a profound change with growth in the relationship of the two pubes to each other. Embryonically the posterior ends are connected by the pubic symphysis and the anterior ends are widespread. But with the loss of the cartilaginous symphysis, the posterior ends of the pubes diverge and the anterior ends converge and may touch in some genera. In the Desmaninae, two genera of which retain the symphysis, this trend is not so noticeable, and in *Sorex* both ends of the one pubic bone remain far apart from those of the other pubic bone. The relationship of these changes to a fossorial life is not completely understood.

It is the closure or near closure of the anterior ends of the pubes which is often incorrectly referred to as the "pubic symphysis." This "pseudosymphysis" occurs dorsal to the viscera and thus excludes them from this part of the pelvic cavity, a fact known to naturalists since at least 1786 (see Leche, 1883: 17, for a historical survey of this literature).

The anterior ends of the pubes are more widespread in *Condylura* than in talpines (Dobson, 1883: 165); those of *Talpa* meet in a pseudosymphysis; of three pelves of *Scalopus aquaticus* available to me the pubes in all were

broadly contiguous; of 46 pelves of *Scapanus* of all ages, sexes, and species investigated by me, eight were closed and 38 were open in varying degrees from 1.0 to 0.1 mm.; the pseudosymphysis of *Scaptochirus* is closed (Chapman, 1919); in a *Mogera wogura* shown by Leche (1883, fig. 32) it is closed, in a *Parascalops breweri* (fig. 35) it is open. Anterior ends of the pubes were separated in all shrews studied by Chapman (1919), as is true in *Sorex*. They are somewhat less separated in *Neürotrichus* (fig. 8D; table 24), *Desmana*, and *Galemys* (Dobson, 1883, pl. 17; Leche, 1883, figs. 22, 25; Puisségur, 1935, fig. 83).

It is the writer's opinion that this general tendency toward narrowness of the anterior pubic region manifest in the more fossorial forms is not an adaptation towards strengthening of the pelvis by the formation of a pseudosymphysis, as such a cross-bracing of the pubes could be of no value until they actually met, and in *Talpa*, one of the most fossorial talpines, they rarely if ever meet. The tendency toward the formation of a pseudosymphysis is actually the secondary result of another talpid alteration, which is the general narrowing of the acetabular region with increased fossorial activity (table 24).

The acetabula in the talpines are probably farther apart in the embryonic stage, but move closer together with age due to a medioventral rotation of the whole mid-portion of the innominate; it is this rotation which secondarily serves to approximate the anterior ends of the pubes.

Whatever the causes, the reduction of the distance between the acetabula has had one clear result; the heads of the femora have been brought closer to the major axis of the body. The sacrum and two innominates are functionally one unit, and any anteriorly directed force applied to one side of this unit, as a force from the femur applied at the acetabulum, will tend to rotate this sacro-innominate unit around its dorsoventral axis. That such rotation does not occur in mammals is due to the compensatory contraction of the long axial muscles which insert upon the sacrum and hold it fast. As the head of the femur is brought closer to the sacrum, however, the rotatory component of the force from the femur is proportionately lessened and the linear component proportionately increased. In respect to these factors the pelves of *Sorex* and *Neürotrichus* are less advantageous to their owners than is that of *Scapanus*.

The common and oft-expressed belief that the pelvis of the mole is narrowed so that the bulky forequarters can pass when the animal turns on itself in its burrow may be partially true, inasmuch as the reduction of the interacetabular distance does decrease the intertrochanteric distance, which is the widest place in the hind quarters. But if one compares the widest part measured in the pelvis of *Scapanus*, the posterior interpubic distance, with the widest part of the pelvis of *Sorex*, which is the interacetabular distance (table 24), it is seen that the difference is so slight as to afford the fossorial animal no advantage; anteriorly the interiliac distance is relatively wider in *Scapanus* than in *Sorex*, and wider in *Neürotrichus* than any measured width of the other genera. Thus one can hardly claim any general relationship between narrowing of the pelvis and a fossorial life; indeed, the distance across the

ischial tuberosities of *Scapanus* (fig. 8B), which was not measured, is probably as great or greater than any transverse distance in the pelves of *Neürotrichus* or *Sorex*.

When one compares the height of the innominate at the acetabulum with the length of the sacrum (this latter value is a relatively constant factor for all three genera), it is found that there is no decrease in the height of the talpid innominate as compared with the soricid, although if one compares this height with the length of the innominate there appears a spurious shortening of the dorsoventral distance at this point in the more fossorial forms (table 24). This supposed relationship is actually due to the differences in innominate length and demonstrates how easily erroneous conclusions may be drawn from illogical premises.

The acetabular fossa of a talpid is somewhat deeper and more regular in outline than is that of *Sorex*, which presents a relatively weak hip-joint. This would add to the evidence that the talpid hind limb delivers a more powerful thrust to the pelvis than does the soricid.

There is a positive correlation (fig. 8) between a decreased size of obturator foramen and an increase in the fossorial mode of life. This decrease has been accomplished by a combination of several factors: (1) dorsoventral thickening of the talpid ischium, which thus encroaches upon the foramen; (2) a more ventral position of the ischium in *Scapanus*, at the expense of the foramen; (3) the posterior margin of the foramen is farther forward in *Scapanus* than in *Neürotrichus;* (4) the elongation of the ilium in the fossorial forms thrusts the acetabulum more posteriorly, thus encroaching upon the foramen. The greater areas of the ischium and of the descending ramus of the pubis afford the talpid more extensive surfaces for muscle attachments; the possible relationship between fossorial activity and the lengthening of the ilium has been discussed; but the relationships between the other factors listed and a fossorial life are not understood.

Every student of the pelvis or of fossorial mammals must consider the paper of Chapman (1919), who found a high positive correlation between fossorial life, parallel position of the sacrum and innominate, and disappearance of the pubic symphysis. Thus the soricoid type of pelvis is paralleled by those of *Chrysochloris*, certain murine and cricetine rodents, and, to a lesser degree, by the geomyid rodents. All these he typified as "fossorial" and stated that the characters of their pelves, therefore, are due to their mode of life. If one classifies the soricoid type of pelvis as "fossorial," then one must classify *Sorex* and certain non-burrowing rodents, such as *Mus*, as fossorial. This is somewhat absurd, and the present writer suggests that the pelves of all small cursorial mammals, as well as fossorial ones, may approach a condition in which the long axis of the innominate tends to parallel the long axis of the sacrum.

In general, Chapman's morphological observations were correct, but his attempts to correlate the evolution of this morphology with the behavior and environment of the animals involved were usually in error. Firstly, he considered all soricoids to be primarily fossorial, whereas *Sorex*, some other shrews,

and probably *Uropsilus* are not; he seems to have based his ideas of the habits of shrews in general solely upon information concerning *Blarina*. The fact that the pelvic types are fundamentally similar in the Soricoidea, therefore, cannot wholly be due to a common mode of life, unless one considers that the thrust of pushing the body through grasses and under the leaf litter is comparable to the thrust of the hind limb by an animal in burrowing.

Secondly, Chapman sought to explain the difference in the wide pelvis of the pocket gopher, *Geomys*, and the narrow pelvis of the moles on the grounds that the gopher throws the dirt out between its legs and then turns around and pushes out the accumulated mass, whereas the mole does not. This statement is incorrect, of course, inasmuch as moles do push the dirt out of the burrow; in any case it would seem to the present writer that, compared to the geomyid type, the narrow talpid pelvis, which brings the heads of the femora close to the vertebral colum, is the more advantageously constructed for receiving and transmitting the thrust from the hind limb in the heavy work of pushing accumulated dirt through a small burrow, and that in this respect the animals have similar habits but divergent morphology, with the mole being more specialized.

Chapman's concept of talpid locomotion and burrowing was incomplete, as can be seen from the following quotation: "The moles press the dirt to the sides and push it upward with the back—literally crawling between the earth particules." It is natural that his ideas of the relationships between talpid behavior and talpid morphology would be vague.

Thirdly, Chapman explained that decussation of the Mm. recti abdomini in certain mammals is dependent upon the lack of a pubic symphysis in those animals, which in turn is due to their fossorial life. There is some correlation between these phenomena, but the causal factors are not so clear. Thus *Desmana* and *Galemys* retain the symphysis, yet have decussation of the muscles; the neotomine wood rats are not fossorial, but have a symphysis and decussation of the muscles (Howell, 1926: fig. 11B and p. 155); *Chrysochloris*, which is a fossorial animal, has neither symphysis nor crossed Mm. recti abdomini (Dobson, 1883: pl. 13, fig. 6; and p. 119), and Chapman attempted an explanation of this exception to his theory on the basis that the gracilis muscles originate on the ventral midline in *Chrysochloris* and form such a support for the viscera that there is no need for the recti abdomini to be crossed; the house mouse, according to Chapman's own figures 10 and 24, has a symphysis but crossed muscles; in the pocket-gopher *Thomomys* the muscles decussate in both males and females although only adult females lose the symphysis (Hill, 1937). Such a list of exceptions to Chapman's conclusions could probably be continued, but those mentioned indicate to the present writer that crossed Mm. recti abdomini, where occurring, must first develop embryonically and the pubic symphysis may later be lost or not, according to the genus involved.

Chapman's confusion as to the presence or absence of a pubic symphysis in female pocket gophers has been explained by Hisaw (1924, 1925), who found that in *Geomys bursarius* the interpubic bar is resorbed in the female at

the time of sexual maturity by the action of an ovarian hormone, which has since been partially purified and termed "relaxin" (see the series of articles by Hisaw and co-workers in Endocrinology, vol. 34, no. 2, Feb., 1944). The presence of such a hormone in adult female monodelphians and its role in absorption of the pubic symphysis in female pocket gophers is illuminating, perhaps, in view of the following statement by Puisségur (1935) concerning *Galemys:* "The females have been obsrved all to be deprived of symphyses, the two pubes leaving between them a short space of a little more than a millimeter. On the contrary, in those males which I have dissected, I find a symphysis uniting the two pubes, slender, of which the cross-section does not exceed a half-millimter." Yet Puisségur's figure 80, purporting to be of the pelvis of a female, shows the pubic symphysis clearly, (Could it have been a virgin female?); no other investigator has noted the lack of symphysis in the female of this genus.

Chapman's general statement that the symphysis tends to move posteriorly as the innominate becomes parallel with the sacrum is true, but his further statement that in such cases it comes to be formed entirely by the ischial bones is not true of the Soricoidea, if Leche's embryological researches are correct.

Chapman's conclusions have been criticized by Todd (1923) on the dual bases that his facts are sometimes incorrect and that he attempts too direct a correlation between pelvic morphology and external environmental influences, when such morphology may actually be due to changes inaugurated by endocrine factors.

On can say that Chapman's paper points out certain interesting relationships, but that his statements must be weighed carefully and that all the factors involved in these relationships have not yet been discovered.

Femur.—Measurements used: (1) Length of femur; the distance from the proximal tip of the femur (this point lies on the head in *Scapanus*, but on the greater trochanter in *Neürotrichus* and *Sorex*) to the midpoint of a line between the most distal lateral and medial points, measured parallel with the long axis of the femur. (2) Proximal breadth of the femur; the distance across the femur between the lesser trochanter and the third trochanter, measured at right angles to the long axis of the femur. (3) Distal breadth of the femur; the greatest distance across the epicondyles, measured at right angles to the long axis of the femur. (4) Breadth of the shaft of the femur; the narrowest transverse breadth of the shaft of the femur. (5) Thickness of the shaft of the femur; the anteroposterior distance through the shaft of the femur, measured at right angles to the breadth of the shaft.

The total length of the femur (table 25) cannot be said to differ among the three genera, although that of the shrew may be slightly shorter. However, if one were to measure the functional length of the femur in *Sorex* and *Neürotrichus*, as was actually done for *Scapanus*, the femur of *Scapanus* would probably be slightly longer than is that of *Neürotrichus* and relatively even longer when compared to *Sorex*. Even so, there would not seem to be enough difference to warrant any conclusions as to functional differences.

The proximal end of the femur is wider and the three trochanters show greater development in the two talpids than in *Sorex* and the trochanters of *Scapanus* show somewhat more development than do those of *Neürotrichus* (table 26). This series would indicate that with an increase in fossorial activity there is greater leverage upon the femur through action of the abductor and rotator muscles inserting upon the trochanters. This increase in leverage,

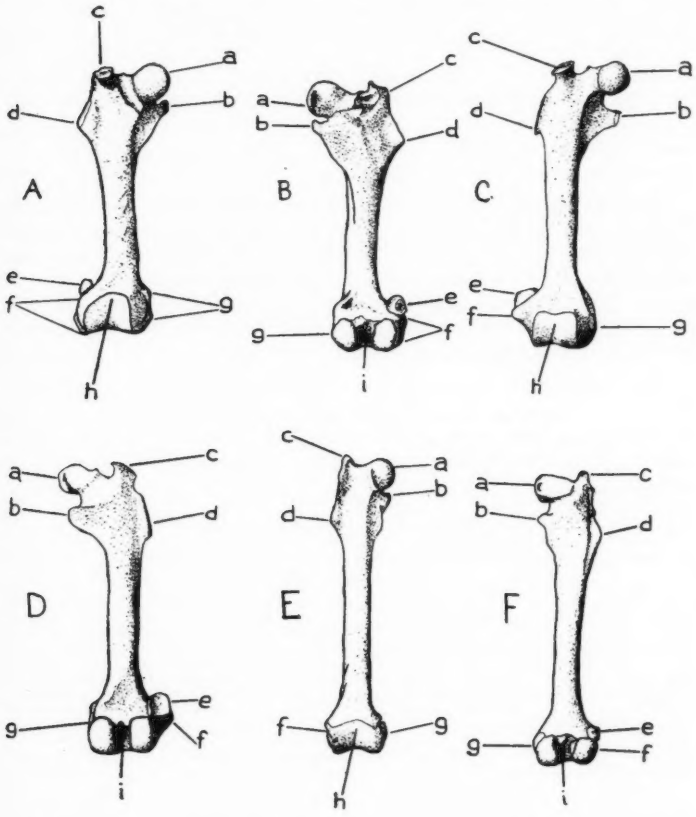

Fig. 9.—A. *Scapanus latimanus*, right femur, anterior aspect, ×2.5. B. Posterior aspect of A, ×2.5. C. *Neürotrichus gibbsii*, right femur, anterior aspect, ×5. D. Posterior aspect of C, ×5. E. *Sorex trowbridgii*, right femur, anterior aspect, ×5. F. Posterior aspect of E, ×5. a, head; b, lesser trochanter; c, greater trochanter; d, third trochanter; e, sesamoid of the lateral epicondyle; f, lateral epicondyle; g, medial epicondyle; h, patellar surface; i, intercondyloid fossa.

in turn, indicates a greater use of the hind limb in a lateral or twisted position by the fossorial forms. Furthermore, this increase in lateral rotatory leverage agrees with the necessity for having the limb in a lateral or twisted position while bracing for burrowing and while pushing dirt through the burrow, and also agrees with the observation of Howell (1923) that *Scapanus*, when running in the burrow, straddles it with the hind feet as well as with the front feet.

TABLE 25.—Relationship between length of femur and length of body

	No.	Mean	σ	V
Sorex	13	11.1 ± 0.2	0.65 ± 0.1	5.85 ± 1.15
Neürotrichus	11	11.6 ± 0.2	0.6 ± 0.1	5.0 ± 1.05
Scapanus	22	11.5 ± 0.15	0.7 ± 0.1	6.25 ± 0.95

The configurations of the heads of the femora differ somewhat. In *Scapanus* the angle between the head and the long axis of the femur is greater than in *Neürotrichus*, and in *Neürotrichus* it is greater than in *Sorex;* these differences probably compensate for the talpid acetabula (especially of *Scapanus*) facing more ventrally than in *Sorex*. Thus the femora can remain parallel to each other in a normal stance without the heads entering the acetabular sockets at different angles in the different genera.

The shaft of the femur is slightly but definitely stouter and rounder in *Scapanus* and flatter and more delicate in *Sorex*, with *Neürotrichus* intermediate (table 26). This series of differences is again probably to be correlated with the greater stresses transmitted through the femur to the pelvis with an increased fossorial life.

TABLE 26.—Proportions of femur

	Proximal Breadth / Length of Femur	Distal Breadth / Length of Femur	Width of Shaft / Length of Femur	Thickness of Shaft / Length of Femur
Sorex	24.4	24.3	10.1	8.4
Neürotrichus	28.5	26.4	10.9	9.5
Scapanus	30.9	25.1	11.5	11.3

The slight differences in distal breadths of the femur do not seem to bear any relationship to differences in function.

The sesamoid attached to the lateral epicondylar ridge serves as a point of origin for the tendons of the Mm. plantaris and gastrocnemius lateralis. The

sesamoid is wide and posteriorly concave in *Neürotrichus*, but more massive in *Scapanus*. In *Sorex* it is small and more firmly attached to the femur.

The condyles of the femur are relatively larger in the two talpids than in *Sorex*, which fact may indicate relatively greater strength in the more fossorial forms; there is no evidence that the knee-joint is more mobile in one form than in another.

In general, it can be said that the femur exhibits few major functional differences, but those present would indicate that the more fossorial the mode of life, the more rugged is the femur and the more developed are the processes upon the proximal end. Of course, these correlations might be due to chance modifications genetically linked with the significant massiveness of the bones of the fore limb.

Shank (Crus).—Measurements used: (1) Length of the tibia; the distance from the most proximal point on the proximal articular surface to the midpoint of a line drawn between the most distal medial and lateral points of the tibia-fibula. (2) Distal breadth of the tibia-fibula; the greatest distance across the distal end, measured at right angles to the long axis of the bone.

Other measurements than these were made on the dimensions of the proximal processes of the tibia and fibula, but since the writer is at a loss to explain the differences exhibited by these processes, and since the drawings of the bones more clearly show such differences than could a table, the measurements and table have been omitted.

TABLE 27.—Relationship between length of tibia and length of body

	No.	Mean	σ	V
Sorex	13	19.3 ± 0.3	1.1 ± 0.2	5.55 ± 1.1
Neürotrichus	4	19.5 ± 0.25	0.5 ± 0.2	2.7 ± 0.95
Scapanus	7	13.6 ± 0.3	0.8 ± 0.2	5.7 ± 1.5

The soricoid tibia and fibula are fused for the distal two-thirds of their lengths, a condition which Winge (1941: 171) believed could be due to a more active condition in the common ancestor. The question, however, is not so simply dismissed, as both fusion and non-fusion of the tibia and fibula are found among mammals of most diverse modes of locomotion. This is not the place for a discussion of this question, but I do wish to point out that elsewhere among the mammals the condition of fusion has arisen independently in several groups; the attempt by Alston (1876) to place together in his "Myomorpha" all rodents possessing this character resulted in an unnatural and heterogeneous assemblage.

The relatively shorter crus of *Scapanus* is an obvious adaptation to a fossorial life; the shorter bone shortens the total length of the hind leg, so that the leg can be more easily manipulated in a burrow, and the shorter crus is an adaptation for power, with a corresponding loss of speed. The true mole has no need of speed, but the power gained by a shortening of the crus

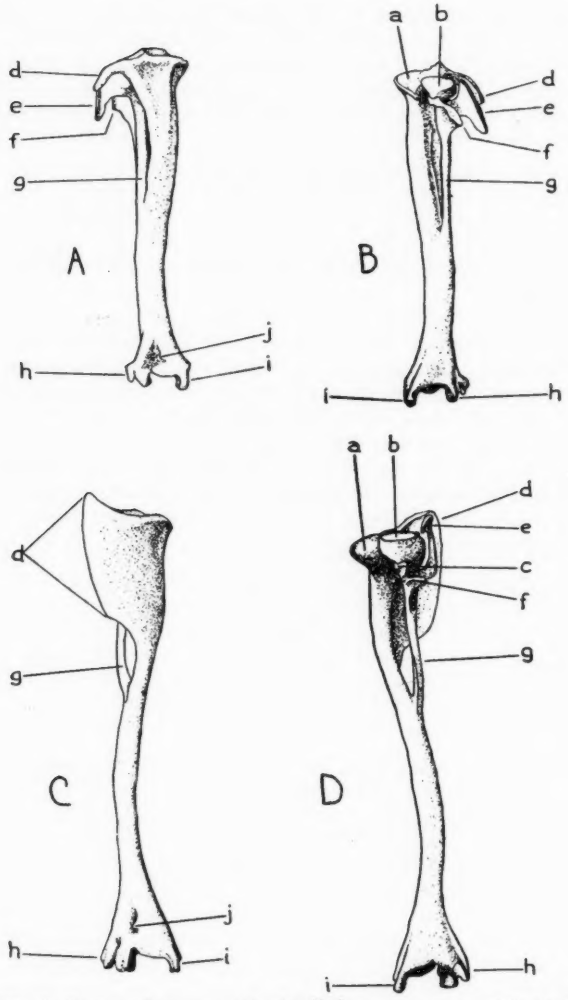

Fig. 10.—A. *Scapanus latimanus*, right tibia-fibula, anterior aspect, ×2.5. B. Posterior aspect of A, ×2.5. C. *Neürotrichus gibbsii*, right tibia-fibula, anterior aspect, ×5. D. Posterior aspect of C, ×5. a, medial condyle of tibia; b, lateral condyle of tibia; c, head of fibula; d, falciform process of tibia; e, lateral process of fibula; f, posterior process of fibula; g, shaft of fibula; h, lateral malleolus; i, medial malleolus; j, ossified portion of transverse crural ligament.

can be applied in extension of the crus, an action important in bracing with the hind feet while tunneling and while pushing dirt out of the burrow.

Neürotrichus, when burrowing, could efficiently use a crus relatively as short as that of *Scapanus*, but when above ground the shrew-mole needs the longer crus for foraging and for greater speed to escape its enemies. The situation is analogous to the relative lengths of the antebrachia, where *Neürotrichus* has long bones for speed, even though shorter bones would be more advantageous in burrowing.

Proximally the anterior crest of the tibia gives rise to a large osseous hook, the "falciform process" of the tibia (figs. 10, 11). In *Sorex* this is directed anteriorly, but in *Neürotrichus* and *Scapanus* it is curved laterally. A further difference is the fact that in *Sorex* and *Neürotrichus* the process is prolonged distally as a wide flange, so thin that in *Neürotrichus* it is almost transparent. These differences influence the origin of the M. tibialis anticus, which in *Scapanus* arises from the process and the anterior surface of the tibia. In *Sorex* and *Neürotrichus* the origin of the muscle is limited to the medial and posterior sides, respectively, of the falciform process, but the course, insertion, and action of the muscle remain the same in all genera. No other muscle originates or inserts upon the falciform process, and no difference in the function of the M. tibialis anticus can be imagined which would so profoundly mold the osseous structure. Actually in *Neürotrichus* only the rim of the posterior side of the falciform process is used for the muscle origin and the greater area of the process has no muscular attachment.

Proximally the head of the fibula exhibits two processes in the talpid genera, whereas the head of the fibula in *Sorex* is entirely without them. These processes have not been hitherto named; I am calling them the "lateral process" and the "posterior process" of the fibula (fig. 10). They are not, to my knowledge, found in other mammals than the talpids. In the talpids these processes give origin to the peroneous muscles (fig. 21), whose origins in *Sorex* cluster around the head of the fibula without benefit of such processes, yet seem to function adequately.

One can postulate, of course, that the peroneous muscles must be larger and more powerful in the talpids, to require such processes; this supposition would fit well with the fact that the peroneous muscles rotate the foot laterally, an action which is used when bracing the pes against the curved walls of the burrow and when running through the burrow.

The postulation of a functional difference in muscular necessities and actions between talpid and *Sorex* does not, however, solve all the questions concerned with these processes. First, much of the area of the processes gives rise to no muscles, but is bare, as is much of the falciform process in all three genera. Why is there developed such size of osseous projections when they are not utilized? Second, the lateral process of *Neürotrichus* is a thin and fragile bar which turns proximally at right angles, to such a distance that its head fits into a groove on the lateral epicondyle of the femur (fig. 11C); any action of the knee-joint swings this projection of the fibula through a wide arc

in this closely fitting groove on the femur. The same two peroneous muscles originate from this process in *Neürotrichus* as in *Scapanus;* there would not seem to be any functional advantage in shifting those origins proximally, for the muscles still run the length of the shank, parallel with it, ot insert almost as in *Scapanus*. Certainly such a delicate process cannot furnish any support to the femur, nor does it have any ligamentous connections to the femur, whereas in *Scapanus* it does. This peculiar configuration of the lateral process of the fibula in *Neürotrichus* I leave entirely without explanation.

One might think that if lateral rotation of the foot is so important to the talpids any muscles of lateral rotation would have been retained and developed; however, the M. peroneous digiti IV, possessed by *Sorex* and *Neürotrichus,* is lacking entirely in *Scapanus*. In general, I have no explanations to offer for the morphological peculiarities of the processes on the proximal ends of the fibula and tibia.

If one disregards the osseous processes clustering around the proximal ends of the tibia and fibula, the knee-joint is normal for small mammals. The anterior and posterior cruciate ligaments are strong; the tibial and fibular collateral ligaments are weaker. The knee-joints of *Sorex* and *Neürotrichus* have been figured from the lateral side (fig. 11); that of *Scapanus* is similar in type to *Neürotrichus*. *Sorex* differs in that a sesamoid is present in the fibular collateral ligament and in that a ligament is present between fibula and tibia. *Scapanus,* moreover, has a weak ligament between the lateral epicondyle of the femur and the proximal tip of the lateral process of the fibula; *Neürotrichus* has no such ligament.

In all three genera the head of the fibula is concave proximally and supports the lateral condyle of the tibia, which supports in turn the lateral condyle of the femur.

The shafts of the tibia-fibula of the three genera are all concave medially, but that of *Scapanus* is straighter, presumably in correlation with the greater stresses withstood by it. Although the breadth and thickness of the shafts were not measured, the shaft of *Scapanus* is obviously thicker and more rugged than are those of *Neürotrichus* and *Sorex*.

Distally the width of the fused bones, as compared to the length of the tibia, is 20.1 per cent for *Scapanus,* 16.2 per cent for *Neürotrichus,* and 12.8 per cent for *Sorex*. Since the greater apparent breadth in *Scapanus* can be attributed to the relative shortness of the bone (table 27), the distal breadths were compared with the lengths of sacra (table 22), which are relatively equal. This procedure yields ratios of 20.5 per cent for *Scapanus,* 20.5 per cent for *Neürotrichus,* and 16.9 per cent for *Sorex*. The distal width of the tibia-fibula of the two talpids is thus shown to be the same, and both are relatively wider than is that of *Sorex;* this relationship is correlated with an actual increased width of foot in the talpids and indicates that the tibia-fibula of *Neürotrichus,* although not modified in length for a fossorial existence, is in part wider and stronger.

The anterior surface of the distal end of the tibia-fibula is grooved for the

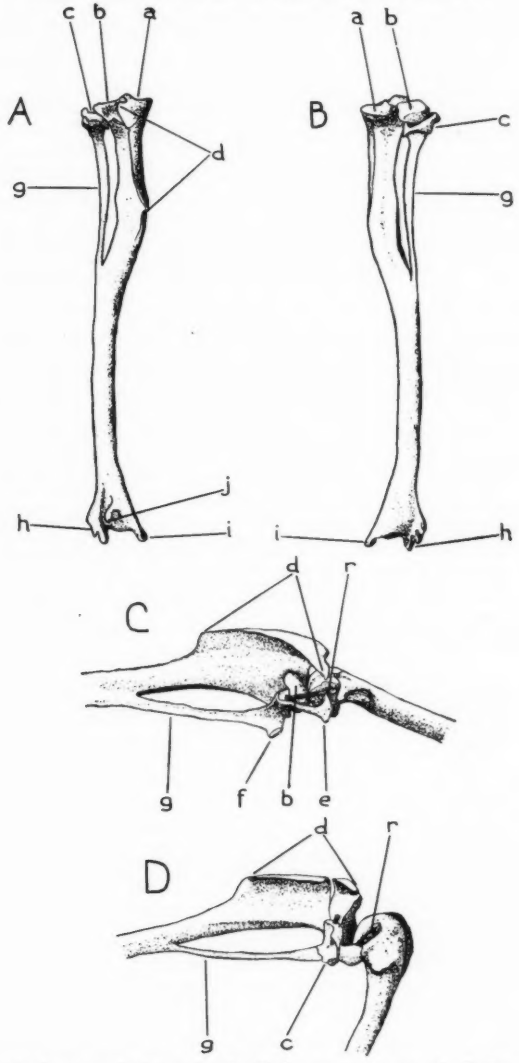

Fig. 11.—A. *Sorex trowbridgii*, right tibia-fibula, anterior aspect, ×5. B. Posterior aspect of A, ×5. C. *Neürotrichus gibbsii*, left knee-joint, lateral aspect, ×5. D. *Sorex trowbridgii*, left knee-joint, lateral aspect, ×5. r, fibular collateral ligament; other abbreviations as in figure 10.

passage of the Mm. extensor digitorum longus, extensor hallucis longus, and tibialis anticus. The muscles run beneath the transverse crural ligament (fig. 22), which originally must have bound together tibia and fibula at their distal ends. This ligament is partly ossified in *Sorex*, somewhat less so in *Neürotrichus*, and hardly at all in *Scapanus* (figs. 10, 11).

Posteriorly the tibia-fibula has two lateral grooves and one medial groove. Of these the most lateral transmits the tendon of the M. peroneus longus; the groove next to it has the tendons of the Mm. peroneus brevis, peroneus digiti V and peroneus digiti IV (the latter not found in *Scapanus*). The medial groove transmits the tendons for the Mm. flexor digitorum tibialis and tibialis posticus.

The lateral and medial malleoli of the tibia-fibula extend down over the edges of the astragalus (talus) in the normal manner, and the ankle-joint is a hinge-joint allowing extension and flexion of the foot in one plane only.

Pes.—Measurements used: (1) Foot length no. 1; the distance from the proximal end of the talus to the distal tip of claw III. (2) Foot length no. 2; the distance from the proximal end of the calcaneum to the distal tip of claw III. (3) Foot breadth; the distance across the distal tips of metatarsals I and V, measured at right angles to the long axis of the foot. (4) Length of the tarsus; the distance from the proximal end of the talus to the middle of the distal articular surface of tarsale III (third cuneiform). (5) Length of metatarsal III. (6) Length of claw III. (7) Length of digit III; the distance from the middle of the proximal articular surface of metatarsal III to the distal tip of claw III.

Since there were few talpid skeletons for which both lengths of foot and lengths of body were available (table 28) the ratios were figured as between all available foot lengths and all body lengths, regardless of the source of the material. For *Neürotrichus* this ratio is 18.9 per cent, for *Scapanus* 14.3 per cent. Thus the figure for the relative foot length of *Neürotrichus* in table 28 would seem to be valid, but for *Scapanus* it might be found to lie, if we had sufficient data, anywhere between 12.0 per cent and 14.5 per cent of the body length. The important thing is that the foot lengths of *Sorex* and *Neürotrichus* are approximately equivalent, but that of *Scapanus* is definitely shorter. This would indicate that, given equal muscular power, the foot of *Scapanus* will deliver more thrust upward through the hind limb than can the foot of the other two genera.

TABLE 28.—Relationship between foot length no. 1 and length of body

	No.	Mean	σ	V
Sorex	14	18.5 ± 0.3	1.2 ± 0.2	6.6 ± 1.25
Neürotrichus	3	19.0 ± 0.8	1.4 ± 0.6	7.2 ± 2.95
Scapanus	2	12.2 ± 0.1	0.2 ± 0.1	1.3 ± 0.65

That the foot of *Scapanus* does deliver more of a forward thrust to the body than in the other types has been indicated, point by point, throughout the osteology of the hind limb.

The long foot of *Neürotrichus* indicates again the dependence of the shrew-mole upon speed when foraging above ground; presumably *Neürotrichus* is not capable in any degree of the power of the forward thrust manifest in the hind limb of *Scapanus*, but, since the shrew-mole does not push dirt through its burrow, such power is not needed.

The foot of all three genera and, so far as I know, of all soricoids, is typical of the primitive mammalian pentadactylous pattern (fig. 12). The only differences lie in the proportions.

Two sesamoids need to be mentioned. The first curves around the medial side of tarsale I (first cuneiform); in the older literature dealing with serial homologies of the tetrapod limbs this sesamoid was always considered the homologue of the falciform bone of the hand. Indeed, Winge (1941: 170) called it the os falciform, as did Dobson (1883: 165), who stated further that this bone is long in *Talpa* and *Mogera*, where it extends forward almost to the distal end of metatarsal I, but it is much shorter in all American moles, and in *Urotrichus* and *Uropsilus*. However, this sesamoid has little relationship to the tibiale, as the os falciforme of the hand has to the radiale, and any idea of analogy, even, is untenable. I am terming it, merely, the "medial tarsale," following Hill (1937: 100). The other sesamoid to be mentioned lies on the proximal end of the plantar surface of metatarsal V in *Scapanus*, IV and V in *Sorex*, and III, IV, and V in *Neürotrichus*. I am terming it the "proximal metatarsal sesamoid"; it lies within a plantar tarsal ligament and serves as origin for some of the intrinsic muscles of the foot. The remaining sesamoids do not require discussion but may be seen in fig. 12.

Since the relationship between the length and breadth of the foot of *Scapanus* (table 29) was calculated on a foot relatively shorter than those possessed by the other two genera, the breadths of foot of all three were compared with the sacral lengths, which are relatively equal. This relationship is 31.2 per cent for *Scapanus*, 27.7 per cent for *Neürotrichus*, and 23.15 per cent for *Sorex*. Thus the foot of *Scapanus* has actually broadened as well as shortened, and that of *Neürotrichus* has broadened, but to a lesser degree, and has not shortened if the condition of *Sorex* be considered as basic. This series indicates, I believe, that with an increase in fossorial activity there occurs a relative increase in necessity for a firm grip upon the substrate and a relative increase in necessity for a broader base upon which to exert the power of the hind leg; this power has presumably increased relative to the broadening and strengthening of the limb elements.

The relatively greater "foot length no. 2" in *Scapanus*, as compared to *Sorex* and *Neürotrichus*, indicates a relatively longer calcar pedis in the true mole. Possibly the calcar did not shorten with the remainder of the foot;

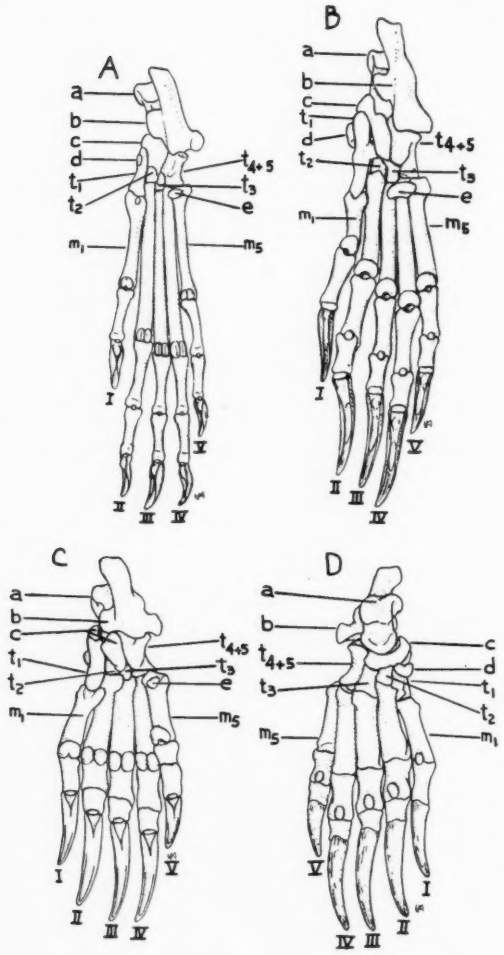

Fig. 12.—A. *Sorex trowbridgii*, right pes, plantar aspect, ×5. B. *Neürotrichus gibbsii*, right pes, plantar aspect, ×5. C. *Scapanus latimanus*, right pes, plantar aspect, ×2.5. D. Dorsal aspect of C, ×2.5. a, talus (astragalus); b, fibulare; c, centrale; d, medial tarsale; e, proximal sesamoid of the metatarsus; m, metatarsal; t, tarsale.

certainly the talpid tarsus did not shorten at as great a rate as did the whole foot. A longer calcar means a more powerful action of the extension of the foot by the Mm. soleus and gastrocnemii, which insert into the calcar by Achilles' tendon. This explains in part the more powerful thrust of the foot for which the whole hind limb of *Scapanus* is adapted.

TABLE 29.—Proportions of the pes

	Foot Length no. 2 / Foot Length no. 1	Tarsal Length / Foot Length no. 1	Claw III Length / Foot Length no. 1	Metatarsal III Length / Foot Length no. 1	Digit III Length / Foot Length no. 1	Foot Breadth / Foot Length no. 1
Sorex	104.5	25.84	14.9	35.6	74.8	17.4
Neürotrichus	104.9	27.2	23.2	26.3	71.9	21.9
Scapanus	109.1	29.5	30.6	21.5	70.4	31.6

Although the manus of *Scapanus* has retained a length relatively equal to those of the other two genera, whereas the pes has not, in general there are remarkable similarities between analogous parts of the two structures if one compare the genera, part by part. In *Scapanus* the breadth of both hand and foot is greatest; the length and breadth of the claws are greatest, so that this is true also for the distal phalanges; and the length of carpus and tarsus is greatest, with a corresponding reduction of length in the metacarpals, metatarsals, and first and second phalanges of hand and foot (tables 11 and 29). For all these factors, also, *Neürotrichus* is intermediate between *Scapanus* and *Sorex*, as it is intermediate between them in locomotor type. Such an array of comparable relationships can hardly be considered coincidental, unless one invokes a theory of linked genetic characters whereby the morphology of the hind limb is automatically patterned after the specialized morphology of the fore limb. To me it does not seem necessary to demand such a theory, as I am of the opinion that the soricoid hind limb is as much a product of natural selection as is the fore limb, even though the purpose of some of the adaptations escape me.

It is interesting that *Neürotrichus*, which retains the long foot for a semicursorial existence above ground, models after the talpine in the proportions of that foot, for fossorial work below ground.

The long claw length in *Scapanus* and, to a lesser degree in *Neürotrichus*, must obviously reduce the power exerted by the long flexors of the pedal digits, and there is no such compensatory factor for greater power for the foot as is furnished to the hand by rotation of the humerus. Perhaps the other adaptational factors in the structure of the foot compensate for this loss of power.

When one compares the length of the tarsus with the length of the foot,

the talpid tarsus is found to be relatively the longest, as the talpid carpus is relatively the longest in the hands of the three genera. Although the causal factors are not evident, I am convinced that there is here some adaptation to a fossorial life. If this be true, one might imagine that the perfect foot for an animal of the diverse styles of life of *Neürotrichus* would be a long foot for semi-cursorial locomotion, but a foot composed of a long tarsus with short digits, for fossorial life. If the soricine condition be taken as basic, *Neürotrichus* has actually developed toward this model foot. If one compares the lengths of tarsi of the three genera with the lengths of sacra, the relationships are: for *Sorex*, 32.8 per cent, for *Neürotrichus*, 34.4 per cent, for *Scapanus*, 31.7 per cent. These figures are rather close, but if they indicate anything it is that the tarsus of *Neürotrichus* has elongated slightly at the expense of the digits, and that the tarsus of *Scapanus* has actually shortened very little, most of the shortening in the foot of *Scapanus* having occurred in the digits. (Of course, *Neürotrichus* may have retained a primitive and generalized type of foot, whereas the foot of *Sorex* may have been modified for a more cursorial life; without a complete fossil series, these things cannot be determined.)

The edges of the soricoid claw do not meet plantarly to cover the distal pedal phalanx, although in *Scapanus* the skin and connective tissue between the edges of the claw is more dense than in *Neürotrichus* or *Sorex*, so that in dried or skeletonized specimens the phalanx is hidden, but by the connective tissue and not by the claw.

There are no dorsal grooves nor bifid extremities to the distal pedal phalanges of any soricoid.

SUMMARY OF THE SKELETON OF THE HIND LIMB

The series available for comparison of lengths of hind limb with lengths of body are too small to be satisfactory for *Neürotrichus* and *Scapanus*, but I will present the evidence for what it may be worth.

TABLE 30.—Relationship between length of hind leg and length of body

	No.	Mean	σ	V
Sorex	13	49.1 ± 0.95	3.4 ± 0.65	6.95 ± 1.35
Neürotrichus	3	49.6		
Scapanus	1	37.5		

The short hind limb of *Scapanus* is due, of course, to the short tibia-fibula and the short foot; the shortness of these bones is an adaptation, as has been shown, for the fossorial life of the true mole. *Neürotrichus* has presumably retained the long hind limb of a soricid type as a necessity for the part of its life above ground, even though the proportions of such a limb may hinder the fossorial portion of its activity.

The difficulty of interpreting comparisons between the length of a limb and the elements of that limb has been mentioned during the discussion of the fore

limb. However, this type of datum is often presented and has been given for the fore limb (tables 19-21), so will be presented here for the hind limb as well.

TABLE 31.—Relationship between length of femur and length of hind limb

	No.	Mean	σ	V
Sorex	25	22.6±0.2	0.9±0.15	4.0 ±0.55
Neürotrichus	9	22.7±0.1	0.3±0.05	1.4 ±0.35
Scapanus	11	29.3±0.2	0.6±0.15	2.05±0.45

TABLE 32.—Relationship between length of tibia and length of hind limb

	No.	Mean	σ	V
Sorex	23	39.2±0.15	0.7 ±0.1	1.8±0.25
Neürotrichus	7	38.4±0.15	0.45±0.1	1.2±0.3
Scapanus	9	35.6±0.2	0.55±0.15	1.6±0.35

TABLE 33.—Relationship between length of pes and length of hind limb

	No.	Mean	σ	V
Sorex	23	37.9±0.15	0.75±0.1	2.05±0.3
Neürotrichus	9	39.0±0.1	0.35±0.1	0.95±0.02
Scapanus	10	38.6±0.3	0.95±0.2	2.50±0.55

Although the adaptations of the sacrum and the hind limb of *Scapanus*, *Neürotrichus*, and *Sorex* to their respective modes of life are not so striking as in the fore limb, nevertheless the hind limb definitely reflects the fossorial life of *Scapanus*, the mixed fossorial and semi-cursorial life of *Neürotrichus*, and the non-fossorial (semi-cursorial) life of *Sorex*. In all the characters to be listed beyond, *Scapanus* has the greatest adaptations for strength of structure or power of leverage, while *Sorex* has the weakest arrangements, with the conditions of *Neürotrichus* being intermediate except where length of limb bones is concerned, in which instances *Neürotrichus* has retained the longer bones of the soricine type for the cursorial part of its life.

Briefly listed, these characters are: the degree of ankylosis of the centra of the sacral vertebrae, the degree of ankylosis of the spines of the sacral vertebrae; the degree of ankylosis between sacrum and innominate, the degree in which the innominate parallels the sacrum, the degree in which the central part of the girdle is compressed and the pubic bones approach each other anteriorly in a pseudosymphysis, the degree of increase in the length of the ilium with a consequent posterior displacement of the acetabulum; the degree of development of the proximal processes of the femur and consequent proximal width of the femur, the degree of stoutness of the shaft of the femur; the relative length of the tibia, the degree of medial concavity of the shaft of the tibia-fibula, the relative size and strength of the shaft of the tibia-fibula, the relative

distal breadth of the tibia-fibula; the relative length of the pes, the relative length of the calcar, the relative breadth of the pes, the relative length and breadth of claws and distal phalanges, and the relative length of metatarsals and first and second phalanges.

The configurations and relative sizes of the falciform process of the tibia and of the lateral and posterior processes of the fibula of *Scapanus* and *Neürotrichus* and the lack of such processes in *Sorex* are not understood.

A statement such as that made by Slonaker (1920) that "the hind legs of the mole are more frail than is usual of a mammal of this size," needs some explanation. What does he mean by "of this size"? After all, the mole is an animal of two sizes; a larger anterior end has been developed on an animal whose posterior end presumably has remained at a more "normal" size. The question of exactly what is the "size" of the mole or any other animal becomes an unsolvable problem, and the best we can do is to compare it with its relatives to establish, if possible, the changes that have occurred with changes in mode of life.

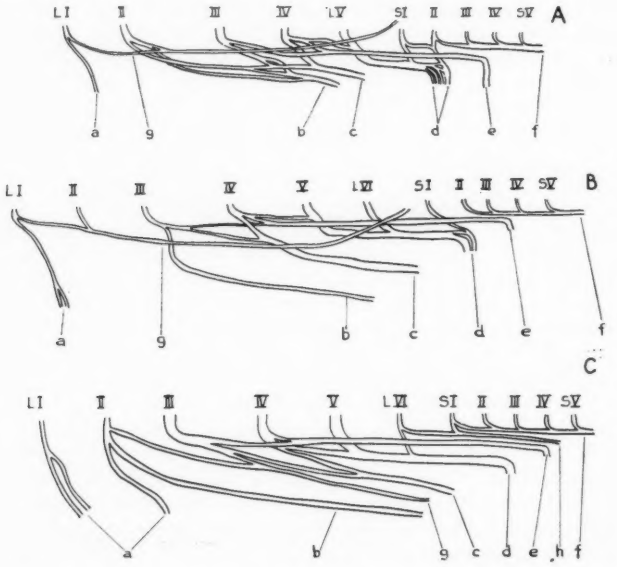

Fig. 13.—A. Lumbosacral plexus of *Scapanus latimanus*. B. Lumbosacral plexus of *Neürotrichus gibbsii*. a, nerve to the anterior abdominal muscles; b, N. cutaneus femoralis lateralis; c, N. femoralis; d, Nn. ischiadicus and pudendus; e, N. obturatorius; f, longitudinal caudal trunk to the tail; g, to the posterior abdominal muscles. C. Lumbosacral plexus of *Sorex trowbridgii*. d, N. ischiadicus; h, N. pudendus; other abbreviations as for *Scapanus* and *Neürotrichus*.

When we do this for the hind limb of the mole (*Scapanus* in this instance) the final conclusion is that the hind limb has become stronger and shorter, and that it undoubtedly has developed a more powerful action. These conclusions are the exact opposite of the concept that the mole's hind limb is weak and frail, a concept held by some authors.

Innervations

The innervation of the fore limb musculature to the elbow was determined in *Sorex, Neürotrichus,* and *Scapanus;* beyond the elbow it was traced only in *Scapanus.* In all these genera the innervation was normal for monodelphian mammals. This innervation has been recorded for each muscle, the nerves are pictured in the muscle drawings, and the brachial plexus of *Scapanus* (fig. 15) is figured.

The statement by Edwards (1937) that the suprascapular and axillary nerves are fused in *Scalopus* is erroneous; since the suprascapular crosses externally to the scapula and the axillary crosses internally to the scapula the two nerves cannot fuse. In all three genera that I dissected I followed these nerves carefully and they run normally; Campbell's (1939) discussion of these nerves disclosed nothing unusual about them.

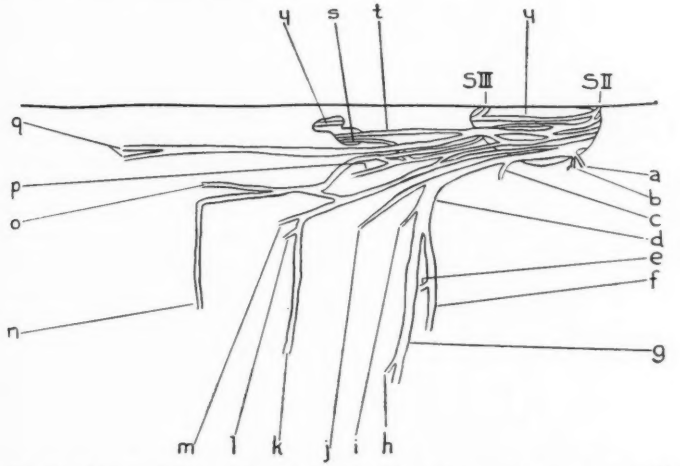

Fig. 14.—Nerves of the lateral aspect of the thigh of *Scapanus latimanus. a,* to M. tensor fascia femoris; b, to M. gluteus medius; c, to M. gluteus maximus; d, N. ischiadicus dorsalis; e, to M. femorococcygeus; f, N. peroneus; g, N. tibialis; h, N. surrae ventralis; i, to M. tenuissimus; j, N. ischiadicus ventralis; k, N. cutaneus femoris posticus; l, to M. biceps femoris; m, to M. semitendinosus I; n, cutaneous to the posterior thigh; o, to M. semitendinosus II; p, to Mm. gemellus and quadratus femoris; q, cutaneous to the dorsolateral side of the tail; s, to M. obturator internus; S II, second sacral spinal nerve; S III, third sacral spinal nerve; t, N. pudendus; y, longitudinal caudal trunk.

In the hind limb the nerves were traced to the knee on *Sorex, Neürotrichus,* and *Scapanus;* beyond the knee the nerves were traced only on *Scapanus.* There is nothing unusual to record for the innervation of the soricoid hind limb; the nerves are pictured in the muscle drawings, the innervation has been recorded for each muscle, the lumbosacral plexus of each genus is illustrated, and a drawing is presented of the nerves of the thigh in *Scapanus.*

Myology

Within recent years the phylogeny of the tetrapod limb muscles has been re-investigated and the more recent evidence disagrees with many of the older ideas. Although the present paper is limited to a single superfamily and is not primarily a study in muscle phylogeny, such notes as are considered useful to the comparative anatomist have been included with the more formal myological descriptions.

For the shoulder and brachium the phylogenetic outlines of Howell (1936b, 1937b) have been followed, since Howell has done the most complete work in this region; Romer (1944) differed from Howell only in relatively unim-

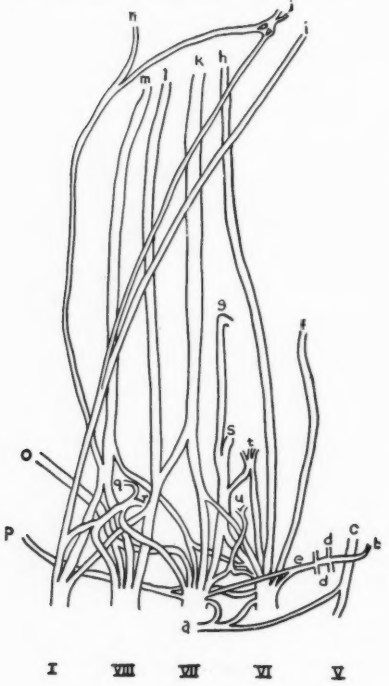

Fig. 15.—Brachial plexus of *Scapanus latimanus.* a, N. phrenicus; b, to M. costoscapularis ventralis; c, N. dorsalis scapulae; d, to Mm. costoscapularis dorsalis and subclavius; e, N. subclavius; f, N. suprascapularis; g, N. axillaris; h, N. musculocutaneus; i, cutaneous branch; j, to M. cutaneus maximus; k, N. medianus; l, N. ulnaris; m, N. radialis; n, to M. dorso-epitrochlearis; o, N. thoracodorsalis; p, N. thoracalis longus; q, to the posterior part of the M. pectoralis superficialis posticus; r, to M. pectoralis profundus; s, to M. teres major; t, Nn. subscapulares; u, to the M. pectoralis superficialis anticus and the anterior part of the M. pectoralis superficialis posticus.

portant details. For the antebrachium and manus I have followed Howell (1936a, b) and Straus (1941, 1942); in those few instances where they disagree, I have followed Straus as being the most recent worker. The paper by Haines (1939) is not so valuable for the problem at hand since it discussed no monodelphian mammal; in any event, its conclusions were subsequently reviewed by Straus (1941).

In the hind limb the situation is more confused. Romer, Appleton, Haines, and Howell have most recently studied this region from the phylogenetic viewpoint. The paper by Haines (1934) can be disregarded insofar as the present work is concerned, as he pointedly ignored innervations; even so, Haine's nomenclature of mammalian thigh musculature differs only in minor details from that of other authors. Romer and Howell disagree on important points; in a recent paper (1942) Romer deplored the lack of a common vocabulary for tetrapod thigh muscles and presented evidence to indicate that some of Howell's conclusions are incorrect. In turn, Howell (1938) admitted Appleton's paper (1928) is difficult to understand; moreover, the latter paper is limited in scope as it treats only of the post-axial thigh muscles. Of the musculature of shank and foot no recent phylogenetic study has been made; the outline by Howell (1936b) reflected the views of Straus, a co-worker, but Straus himself has not published his complete studies on this region. A review of the long extensors of the mammalian hind foot by Hunter (1925) completely ignored the Insectivora.

Since many problems in the hind limb are yet unsolved, I have arbitrarily followed the phylogenetic outlines as presented by Howell (1936a, 1938), being fully aware that further work may modify Howell's conclusions, as Romer's studies (1942: 286-287) have already done in part. In addition I have used Appleton (1928) and especially Leche (1883) as references for determinations of homologies and for discussions of individual muscles.

The papers on soricoid anatomy have already been reviewed (p. 516); to summarize the myological investigations of these authors and to clarify future comparisons between these papers, tables of myological synonymy are here presented (tables 35, 36). Within each column words in quotations are direct statements from the paper in question, but words in parentheses are my own notations.

The dorsal (extensor) and ventral (flexor) musculature of each limb will not be discussed completely as separate units, but the discussion will be interrupted at the elbow and at the knee, respectively, so that the shoulder, the antebrachium and manus, the thigh, and the shank and pes can be treated as units. This procedure may not be logical from a phylogenetic viewpoint, but is topographically convenient.

Dissection of the fore limb began with *Sorex*, proceeded to *Neürotrichus*, and was concluded with *Scapanus*. Unless one follows through such a soricoid series from a generalized form to the more specialized, the correct determination of talpine structure would be extremely difficult, as the muscles and

nerves are so changed in position that their identification is not easy. To illustrate my discussion of the fore limb, drawings are presented of *Neürotrichus;* various views of the fore-limb musculature of *Blarina, Crocidura, Desmana, Condylura, Scalopus,* and *Parascalops* have already been presented by others.

In the hind limb, dissection began with *Scapanus* and was concluded with *Sorex,* since the muscles of this region vary but little within the genera studied and the largest form was the easiest upon which to begin; figures are based on it.

Before proceeding with the myological description it should be mentioned that the animal used by Dobson (1883) as his desmanine type was *Desmana,* and not *Galemys* as Campbell (1939) thought. Dobson clearly labeled his specimens *Myogale moschata,* which was the name for the Russian desman. If he had been dissecting *Galemys,* the Iberian desman, he would have called it *Myogale pyrenaica.* Moreover, Dobson's plates of his *Myogale* show the flattened tail of *Desmana* and not the round tail of *Galemys.*

MUSCLE VOLUMES

After the volume of each muscle had been measured (p. 519), the total volume of each limb was calculated and the percentage relationship established between this total volume and each muscle in the limb.

Even after this procedure, the analysis of such data is difficult, since, for each value determined, one is dealing with a comparison between one variable and the summation of many variables. Any change in size in any muscle changes the relative size of each other muscle in the limb, so that if one muscle group in one genus is extremely changed, as the rotators of the humerus are hypertrophied in *Scapanus,* the relative sizes of the other muscles in the limb undergo compensatory changes in the percentage relationships they bear to the limb as a whole. And when not one group, but every muscle in every group may bear a different relationship to the limb in different genera, the direct comparison of percentage relationships of one muscle between genera may lead to erroneous conclusions. One can only compare trends between genera, since there is no standard measurement (as length of body was a standard for linear measurements) to serve as a direct basis of comparison.

In general the results of the determinations of muscle volumes were disappointing due to the errors inherent in the handling of such small muscles and due to the difficulty of understanding the data. For the hind limb the volumes, as measured for different genera, proved to be so variable for any muscle group that no conclusion are justified; it is suspected that for some measurements the error was greater than the true volume. In any event the successful analysis of the muscle volumes of the soricoid hind limb awaits the dissection of a larger number of specimens and the measuring of the volumes of the muscles more accurately than has been accomplished to date; such data as have been gathered in this study will not be presented in this paper.

For the fore limbs of *Neürotrichus* and *Scapanus* the results are more satisfactory, but data for *Sorex* are incomplete inasmuch as some of the muscle

TABLE 34.—Muscle volumes

Muscle	Individual Muscles, *Scapanus*	Muscle Groups, *Scapanus*	Muscle Groups, *Neuritrichus*	
Trapezius anticus			2.38	
Trapezius medius				
Rhomboideus posticus			1.78	
Trapezius posticus	0.79	0.79	2.38	
Rhomboideus capitis	1.64	2.58	2.98	
Rhomboideus cervicis	0.85			
Serratus anterior thoracis	2.70	2.70	5.95	
Latissimus dorsi	6.87		4.17	
Teres major	23.25	55.23	15.77	45.83
Subscapularis	10.57		14.88	
Pectoralis posticus	14.53		11.01	
Spinodeltoideus	3.44			
Pectoralis anticus	3.49	6.92	9.82	
Infraspinatus	0.58			
Acromiodeltoideus	0.58	0.95	1.19	
Cleidodeltoideus	0.37			
Costoscapularis ventralis	2.17	4.02	5.65	
Costoscapularis dorsalis	1.85			
Pectoralis profundus	1.37	1.37		
Supraspinatus	0.85	0.85	2.38	
Brachialis	1.64			
Biceps brachi	1.06	3.84	2.98	
Supinator	0.01			
Pronator radii teres	1.37			
Triceps	11.12			
Anconeus lateralis	0.95	13.00	11.31	
Epitrochleo-anconeus	0.92			
Palmaris longus	0.53			
Fl. digitorum profundus	2.64			
Fl. digitorum sublimus	0.08	3.70	2.68	
Fl. carpi radialis	0.03			
Fl. carpi ulnaris	0.42			
Ext. indicis et pollicis longus	0.53			
Ext. digitorum communis	1.19			
Ext. digiti quinti proprius	0.37	3.57	2.68	
Ext. carpi ulnaris	0.13			
Ext. carpi radialis	0.77			
Abd. pollicis longus	0.58			

groups have a volume less than 0.001 cc. and could not be measured. The only comparisons of muscle volumes, therefore, that are considered to be of any value are between the fore limbs of *Scapanus* and *Neürotrichus* (table 34).

The useful data salvaged from the calculations for the hind limb are comparisons derived by the division of the volume of the total hind limb musculature by that of the total fore limb musculature. For *Sorex* this value is 88.7 per cent, for *Neürotrichus* 34.5 per cent, and for *Scapanus* 14.9 per cent. These figures probably are not accurate, but they do indicate the tremendous increase of the fore limb musculature over that of the hind limb musculature with increase in fossorial activity.

The foregoing table presents the data for the muscle volumes of the fore limbs of *Scapanus* and *Neürotrichus*. The muscles of *Neürotrichus*, to be measured, had to be grouped according to their functions, but for *Scapanus* the percentage values of both the individual muscles and the functional groups are presented. A further source of difficulty in comparisons between the two genera lies in the lack of Mm. trapezius anticus and trapezius medius in *Scapanus* and of the M. pectoralis profundus in *Neürotrichus;* the M. rhomboideus posticus could not be successfully removed in *Scapanus*, nor was the M. subclavius removed in either genus.

The M. teres major and subscapularis are almost the same size in *Neürotrichus*, but the former muscle is more than twice the size of the latter in *Scapanus*. This difference is at least partly due to the usurpation in *Scapanus* by the M. teres major of much of the area of origin occupied by the M. subscapularis in *Neürotrichus*.

There is an interesting relationship between rotators and counter-rotators of the humerus. In *Scapanus* the great rotators have hypertrophied more than in *Neürotrichus*, so that the counter-rotators (Mm. spinodeltoideus, pectoralis superficialis anticus, and infraspinatus) appear to be relatively reduced in *Scapanus;* they might, however, be shown to be the same relative size in the two genera if there were a direct standard of comparison. One would imagine that the counter-rotators of *Scapanus* could not be reduced much, if at all, and still function, since the sheer bulk of the fore limb must require a certain modicum of muscle to operate, even on the recovery stroke after a digging stroke. The extremely small size of the M. infraspinatus in *Scapanus* is in correspondence with the tendency for its atrophy in talpines.

In *Scapanus* the M. supraspinatus is also reduced relative to the size of the fore limb. This decrease is so marked that it may represent an actual, as well as a relative, decrease in size of the muscle. If this is true, a part of the normal function of this muscle, extension of the humerus anteriorly, must be performed by the M. pectoralis superficialis anticus.

The reduction in bulk of the trapezius group in *Scapanus* is due, at least in part, to the complete absence of the Mm. trapezius anticus and trapezius medius. Whether or not the M. trapezius posticus has changed in size cannot be known.

A comparison of the flexors and extensors of the antebrachium shows only that both sets of muscles in *Scapanus* have hypertrophied to a greater degree, in comparison with all the muscles of the fore limb, than they have in *Neürotrichus*, but the relationship between extensors and flexors is about the same in each genus.

The condition of the extensors and flexors of the manus is similar to that of the extensors and flexors of the antebrachium; both sets of muscles are hypertrophied in *Scapanus* as compared to *Neürotrichus*, but the relationship between the two groups of muscles is approximately the same in each genus. The greater part of the flexor "musculature" in both genera is composed of the great ligament of the M. flexor digitorum profundus; in *Scapanus* it is my observation that this ligament is relatively increased in size, and the actual musculature relatively decreased, as compared to the same muscles in *Neürotrichus*.

It is interesting to note the extremely small size of many of the extensor and flexor muscles of the manus of *Scapanus;* the same would be true for *Neürotrichus* if they could be measured separately. Some of these (Mm. flexor digitorum sublimus, flexor carpi radialis, extensor carpi ulnaris) are so small that it does not seem possible that their contractions can effect movement of the hand.

There is a direct correlation between the sizes of the muscle masses of the fore and hind limbs and the sizes of the centers of the cerebellum which coordinate actions of these muscle masses (Larsell and von Berthelsdorf, 1941). This region, the lobulus anseriformes of the cerebellum, not only varies directly in its total area with the total mass of both limbs, but is divided into two regions, an anterior Crus I which controls the fore limb, and a posterior Crus II which controls the hind limb. In *Scapanus*, according to Larsell and von Berthelsdorf, Crus I represents 72.3 per cent of the anseriform lobe, Crus II 27.7 per cent. Similarly in bats, where the fore limb musculature constitutes an even greater part of the total limb musculature than it does in moles, Crus I is 83.2 per cent of the anseriform lobe. Conversely, in rabbits, where the hind limb musculature is greater than that of the fore limb, Crus II is larger than Crus I. Thus correlated evolutionary changes in limb proportions and locomotor behavior can be related directly to changes in the areas of the cerebellum controlling those muscle masses. One would expect to find comparable correlation with the sizes of the motor areas of the cerebrum of these same animals.

THE HIND LIMB

MYOMERIC MUSCULATURE

Lateroventral division—Appendicular system (pelvic limb)

PREPELVIC COMPONENTS (Hip and Thigh),

DORSAL DIVISION (N. femoralis group)

M. psoas major (figs. 16, 17, 19).—In *Scapanus, Neürotrichus,* and *Sorex* the origin is from the ventrolateral surfaces of the posterior three or four lumbar vrtebrae, from the first sacral vertebra, from the dorsal surface of the extreme posterior part of the tendon

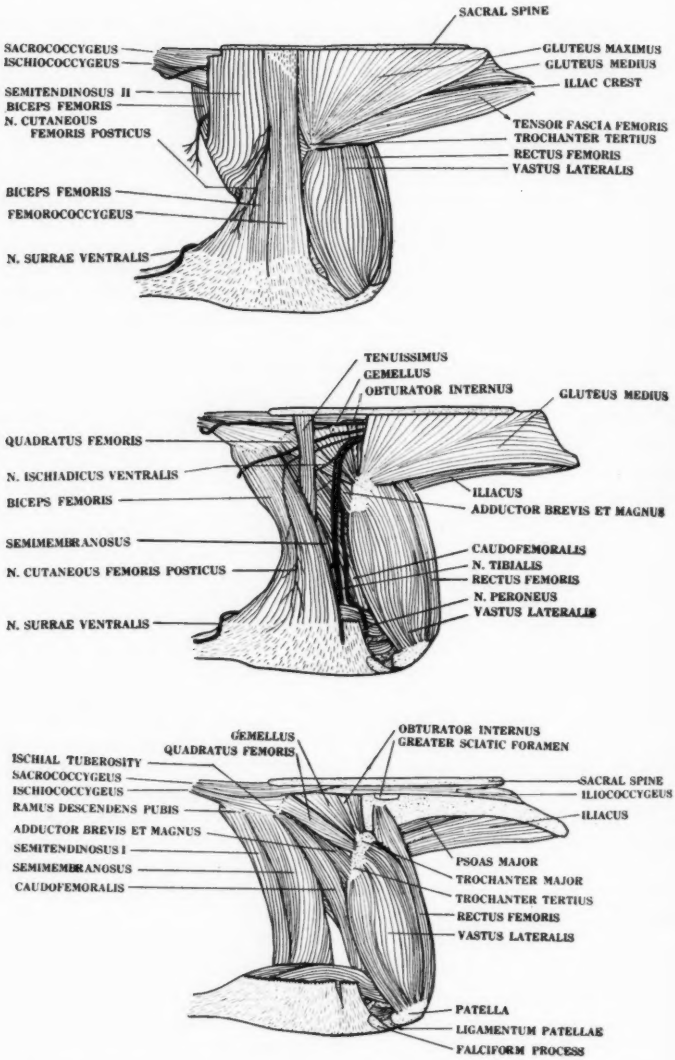

Fig. 16.—Thigh musculature of *Scaparus latimanus*, lateral view. A. Superficial layer, ×2. B. Intermediate layer, ×2. C. Deep layer, ×1.9.

of the M. psoas minor, and, by a few fibres, from the ilium adjacent to the point of insertion of the tendon of the M. psoas minor. The M. psoas major is more or less fused with the iliacus; the tendons of the two muscles run parallel and insert side by side, but the main trunk of the N. femoralis separates the muscles. The muscle inserts by a strong tendon and by muscular fibers on the tip of the lesser trochanter of the femur.

Action. Flexor and rotator of the femur.

Discussion. Leche (1883) treated the Mm. iliacus and psoas major under one name, the M. iliopsoas.

M. psoas minor (fig. 17).—This is a long, slim muscle which originates in *Scapanus* from the ventrolateral surfaces of the first, second, and third lumbar vertebrae. The muscle is tendinous posterior to the level of the last lumbar vertebra; the narrow tendon inserts on the median side of the iliopectineal process of the ilium.

In *Neürotrichus* the origin is from the second lumbar vertebra only; some of these fibers join the M. psoas major. The tendon of insertion is accompanied by some muscle fibers to its insertion; otherwise the muscle is as in *Scapanus*. In *Sorex* the origin is from the fourth lumbar vertebra, otherwise the muscle is as in *Scapanus*.

Action. Contraction of both muscles simultaneously would arch the posterior portion of the back by approximation of the ilia to the anterior lumbar vertebrae.

Discussion. Leche (1883) stated that this muscle is always more or less fused with the M. iliopsoas; in the genera dissected by me this is true only in the sense that some of the fibers of the M. psoas major originate from the tendon of the M. psoas minor. Howell (1936b) thought the M. psoas minor might be part of the hypaxial division of the axial musculature; in 1938 the same author considered more likely the hypothesis that this muscle is an associate of the M. psoas major and iliacus, as here indicated.

M. iliacus (figs. 16, 17, 19).—In *Scapanus* this prismatic muscle originates from the ventral and posterior surfaces of the transverse process of the most posterior lumbar vertebra, from the ventral surface of the first sacral vertebra, and from the ventral surface of the anterior half of the ramus of the ilium, lateral to the origin of the M. psoas major from the ilium. The muscle narrows posteriorly to its tendon of insertion upon the tip and anterior surface of the lesser trochanter of the femur, distal to the point of insertion of the M. psoas major.

In *Neürotrichus* the muscle is divisible into two parts; the one which takes origin from the ventrolateral surface of the ramus of the ilium is closely associated with the M. psoas major and inserts with that muscle by a common, fused tendon. The part of the M. iliacus which originates from the transverse processes of the fifth and sixth lumbar vertebrae and from the iliac crest runs parallel and lateral to the part first described and inserts by a separate tendon adjacent to, but immediately distal from, the first part.

In *Sorex* the muscle originates from the same surfaces as it does in *Neürotrichus*, but all the heads of origin fuse together into one muscle which inserts upon the medial surface of the shaft of the femur immediately distal to the lesser trochanter.

Action. The muscle is a flexor and rotator of the femur, acting in conjunction with the M. psoas major.

M. sartorius.—There was no M. sartorius in any specimen dissected. According to Leche (1883: 85) the M. sartorius occurs only in *Tupaia* and *Erinaceus* among the insectivores. The muscle termed "sartorius" by Dobson (1883) in *Desmana* and *Condylura*, and labeled as such in his figures, is innervated by the N. obturatorius, not by the N. femoralis, and is therefore the M. gracilis.

M. quadriceps femoris (figs. 16-19).—This muscle may be considered to originate by four heads, which fuse in a common insertion. In *Neürotrichus* and *Scapanus* the M. rectus femoris originates from a shallow depression immediately anterior and dorsal to the acetabulum. The more distal part of the muscle receives many fibers from the anterior part of the Mm. vastus medialis and vastus intermedius. In *Sorex* the origin of the M. rectus femoris does not lie so far dorsally.

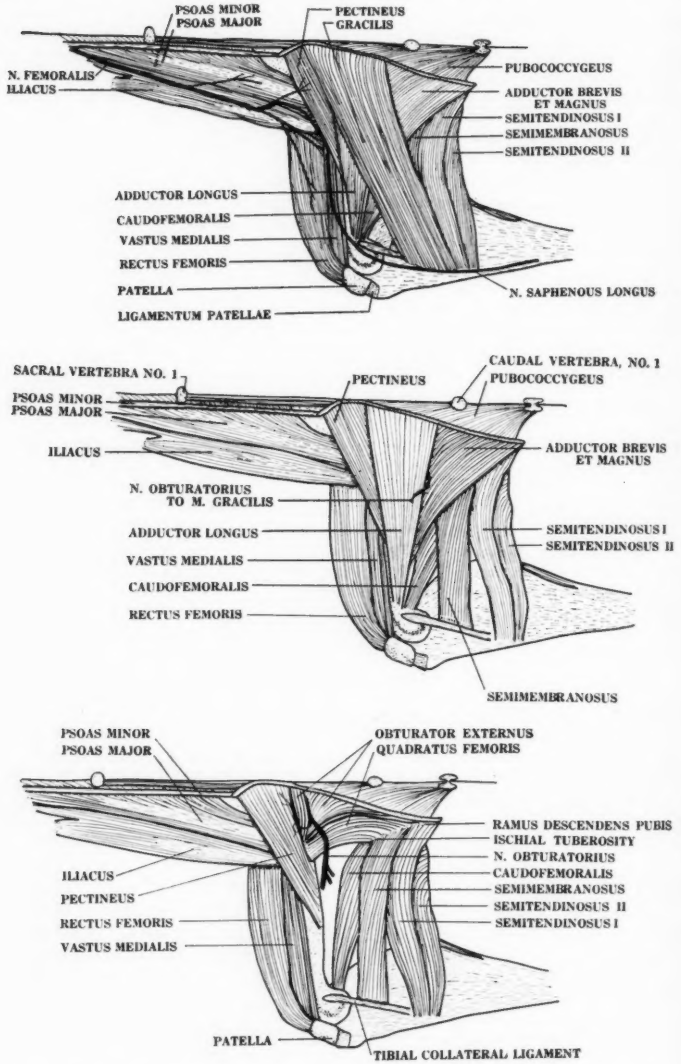

Fig. 17.—Thight musculature of *Scapanus latimanus*, medial view. A. Superficial layer, ×2.15. B. Intermediate layer, ×2.2. C. Deep layer, ×2.2.

In all three genera dissected the origin of the M. vastus lateralis is from the anterolateral rim of the greater trochanter, from the anterior side of the ridge between the greater and third trochanters, and from the anterior rim and lateral side of the third trochanter.

In all three genera dissected the origin of the M. vastus medialis is from the anteromedial side of the shaft of the femur, between the neck and the distal fourth of the femur. Although the muscle is extensively fused with the adjoining fibers from the posterior side of the rectus femoris, the greater part of the muscle fuses with the M. vastus lateralis. The most posteromedial fibers of the M. vastus medialis insert separately and fleshily into the patella. The deeper part of the M. vastus medialis can be separated as a M. vastus intermedius; the origin is continuous with that of the M. vastus medialis and these deeper fibers insert either with the M. vastus lateralis or directly upon the patella.

All the M. quadriceps femoris, other than the parts noted as exceptions, fuses into a common mass and inserts upon the patella and through the patella and the patellar ligament upon the anteroproximal surface of the tibia. From the patella a smaller ligament, deep to and lateral to the patellar ligament, inserts into the synovial membrane and bursa of the anterior side of the knee joint; this ligament of insertion corresponds to the lateral retinacula of man.

Action. The M. quadriceps femoris is the great extensor of the shank.

PREPELVIC COMPONENTS (Hip and Thigh)

VENTRAL DIVISION (N. obturatorius group)

M. obturator externus (figs. 17-19).—In *Scapanus* this muscle originates from the lateral edge of the whole length of the horizontal ramus of the pubis. The muscle is separable into two parts, of which the posterior is twice the size of the anterior; the obturator nerve emerges from the obturator foramen and between the two parts of the muscle. The fibers of this small, flat, triangular muscle aggregate to insert into the intertrochanteric fossa of the femur.

In *Neürotrichus* the muscle is not so clearly separable into two parts; the obturator nerve pierces the muscle instead of separating it. In *Neürotrichus* the origin is more extensive than in *Scapanus*, since, in addition to the area of origin of the muscle in *Scapanus*, it originates from most of the obturator membrane and from the ventral edge of the descending ramus of the pubis.

In *Sorex* the anterior and posterior parts of the muscle are separate, as in *Scapanus*, but the muscle as a whole is so fused with the Mm. quadratus femoris and gemellus that it cannot be distinguished as an individual muscle; in *Scapanus* and *Neürotrichus* there is no fusion with any other muscle.

Innervation. Both heads are innervated by the obturator nerve; this innervation does not agree with Leche's (1883) statement that the posterior head was supplied by the ischiadic nerve in *Talpa* (although in *Crocidura* he stated that it was innervated by the obturator nerve).

Action. Retractor and rotator of the femur.

Discussion. The part of this muscle which lies anterior to the obturator nerve was termed the M. obturator intermedius by Leche (1883: 79), who recognized, however, its affinity with the M. obturator externus. This name for this part of the muscle has not gained acceptance.

M. pectineus (figs. 17-19).—In *Scapanus*, *Neürotrichus*, and *Sorex* this flat, triangular muscle originates from the iliopectineal process and the adjacent ilium and pubis. The fibers run distally and slightly posteriorly to insert on the medial surface of the lesser trochanter and the proximal half of the shaft of the femur. In *Sorex* the insertion extends farther distally on the femur.

Innervation. The anterior part of the muscle is innervated by the femoral nerve, the posterior part by the obturator nerve. Howell (1936b) suggested that the motor axons to the anterior part of the muscle had somehow shifted from the obturator to the femoral nerve and that no part of the muscle basically belonged to the femoral group.

TABLE 35.—Muscles of the thigh

Leche, Insectivora	Dobson, Talpidae	Appleton, Mammalia	Howell, Monodelphia	Reed, Soricoidea
1. Tensor fascia latae	(Included with M. gluteus maximus)	Tensor fascia latae	Tensor fascia femoris	Tensor fascia femoris
2. Gluteus maximus	Gluteus maximus	Gluteus superficialis	Gluteus maximus	Gluteus maximus
3. Gluteus medius	Gluteus medius	Gluteus medius	Gluteus medius	Gluteus medius
4. Femoro coccygeus	Anterior superficial head, Biceps flexor cruris	Femoro coccygeus	Gluteus longus	Femoro coccygeus
5. Biceps femoris	Deep head, biceps flexor cruris	Biceps	Biceps	Biceps femoris
6. Tenuissimus	Anterior deep head, biceps flexor cruris	Tenuissimus	Tenuissimus	Tenuissimus
7. Gracilis	Sartorius	————	Gracilis	Gracilis
8. Adductor longus	Adductor longus	————	Adductor longus	Adductor longus
9. Adductor brevis et magnus	Adductor brevis	————	Adductor brevis, and Adductor magnus	Adductor brevis et magnus
10. Pectineus	Pectineus	————	Pectineus	Pectineus
11. Praesemimembranosus (or) Caudofemoralis	Adductor magnus	Caudofemoralis	Praesemimembranosus (= Caudofemoralis)	Caudofemoralis
12. Semimembranosus	Semimembranosus	Semimembranosus	Semimembranosus	Semimembranosus
13. Semitendinosus I	Gracilis	Flexor cruris, caput ventrale	Semitendinosus	Semitendinosus I
14. Semitendinosus II	Semitendinosus	Flexor cruris, caput dorsale		Semitendinosus II

Action. The muscle is primarily an adductor of the femur, but would also aid in flexion of the extended femur.

M. gracilis (figs. 17, 18, 21).—In *Scapanus, Neürotrichus,* and *Sorex* the muscle originates from the ventrolateral margin of the horizontal ramus of the pubis between the iliopectineal process and the midpoint of the horizontal ramus. The wide, flat muscle runs distally and slightly posteriorly to insert on the proximal portion of the anterior crest of the tibia.

Action. Flexor of the crus, adductor of the hindlimb.

Discussion. In dissection, the muscle is easily removed with the fascia of the medial side of the thigh, and thus overlooked. Dobson (1883) mistook the M. gracilis for the M. sartorius and assigned the name "gracilis" to the M. semitendinosus I.

M. adductor longus (figs. 17-19).—In *Scapanus, Neürotrichus,* and *Sorex* this flat, triangular muscle originates from the ventrolateral edge of the middle part of the horizontal ramus of the pubis, deep to the origin of the M. gracilis but covering the origin of the anterior part of the M. adductor brevis et magnus. The fibers run distally and insert in two parts; the distal of these has the longest fibers and inserts on the proximal surface of the medial epicondyle at the junction of the epicondyle and the shaft of the femur. The proximal part, which is deeper, inserts on the distal two-thirds of the posterior surface of the shaft of the femur.

Action. The muscle is an adductor of the femur and would serve to extend the femur when it was flexed against the abdomen.

Discussion. Leche (1883) noted distal and proximal insertions for *"Myogale,"* but not for true moles. Dobson (1883) described both insertions for *Desmana,* but mentioned only the distal insertion for *Condylura;* presumably *Condylura* has both insertions, however.

M. adductor brevis et magnus (figs. 16-19).—These two muscles are fused into a single entity in the soricoids (Leche, 1883: 82). In *Scapanus, Neürotrichus,* and *Sorex* the muscle originates from the lateral surface of the posterior half or two-thirds of the horizontal ramus of the pubis and continues on to the descending ramus of the pubis. The fibers of the triangular muscle aggregate anteriorly and distally to insert, in *Scapanus* and *Neürotrichus,* along the posterolateral surface of the femur between the third trochanter and the level of the sesamoid of the lateral epicondyle of the femur. In *Sorex* the insertion is more proximal, between the levels of the greater and third trochanters, so that contraction of the muscle would produce much faster movement of the femur, with a corresponding loss of power.

Action. Adductor and extensor of the femur.

Discussion. Dobson (1883) termed this muscle the M. adductor brevis; the M. caudofemoralis he called the M. adductor magnus. The muscle termed "caudofemoralis" by Leche, Appleton, and myself is innervated by the N. ischiadicus ventralis and thus cannot be one of the adductor group, all of which are innervated by the obturator nerve.

TABLE 35.—Muscles of the thigh

APPENDICULAR SYSTEM (PELVIC LIMB)
POSTPELVIC COMPONENTS (Hip and Thigh)
DORSAL DIVISION (N. peroneus group)

M. gluteus maximus (figs. 16, 18, 19).—In *Scapanus* the origin of this muscle is always from the crest of the sacral spines of the anterior four sacral vertebrae and the anterior half of the fifth sacral vertebra. In addition the muscle may take origin in variable degrees from the lumbodorsal fascia between the anterior tip of the sacral spine and the crest of the ilium, or this part of the origin may be present but be largely fascial. If the origin extends upon the crest of the ilium, the Mm. gluteus maximus and tensor fascia femoris are fused throughout their lengths but can always be distinguished by a slight difference in the direction of their fibers. In addition, the posterior part of the M. gluteus maximus takes origin from the dorsal part of the lateral surface of the sacral spine and from the deep surface of the tendon of origin of the M. femorococcygeus. The posterior

part of the muscle is thicker and stronger than is the anterior. The fibers aggregate distally and insert upon the tip and proximal surface of the third trochanter.

Innervation. N. gluteus inferiorus.

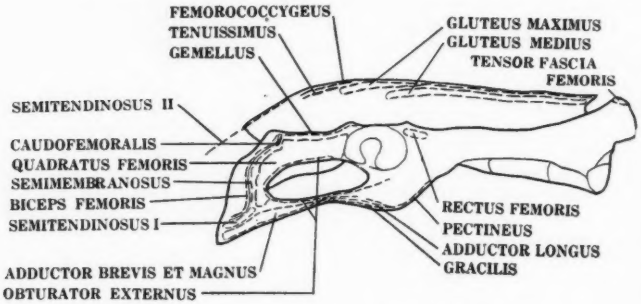

Fig. 18.—Pelvis and sacrum, lateral view, right side, *Scapanus latimanus*, showing areas of muscle attachments, ×2.5.

Action. Abductor and rotator of the femur; the extent and type of action would depend upon which part of the muscle contracted, since fibers insert both anterior and posterior to the long axis of the femur.

Discussion. Leche's (1883: 68) statement that the M. gluteus maximus inserts upon the greater trochanter in *Talpa* is at variance with the condition as found by myself in *Scapanus*, *Neürotrichus*, and *Sorex*, and as found by Dobson (1883) in *Desmana* and *Condylura*.

In *Neürotrichus* the lateral margin of the M. gluteus maximus and the medial margin of the M. tensor fascia femoris are always fused and the two muscles are more difficult to separate than in *Scapanus*. In *Sorex* the sacral part of the origin is from the three anterior sacral spines only.

M. tensor fascia femoris (figs. 16, 18, 19).—In *Scapanus*, *Neürotrichus*, and *Sorex* the origin is from the crest of the ilium, superficial to all other muscles. The fibers run posteriorly and slightly distally, lateral to the M. gluteus maximus and covered posteriorly by the edge of that muscle, to insert upon the anterior side of the third trochanter.

Innervation. Branch of the N. gluteus superioris; the branch to the M. tensor fascia femoris passes beneath the M. gluteus medius, between the muscle and the dorsal surface of the ilium, and enters the M. tensor fascia femoris on its ventral surface.

Action. Flexor and rotator of femur.

Discussion. Howell (1936b) stated that this muscle is a derivative of the M. gluteus medius; the innervation by the superior gluteal nerve of both muscles in the soricoids supports this view.

M. gluteus medius (figs. 16, 18, 19).—In *Scapanus*, *Neürotrichus*, and *Sorex*, this muscle originates from the posterodorsal surface of the crest of the ilium with a few shorter fibers coming from the dorsolateral edge of the ramus of the ilium, from the lumbodorsal fascia between the anterior end of the sacral spine and the crest of the ilium (Leche says also from the last lumbar vertebra in talpids, but I did not see this), and from the dorsal part of the lateral surface of the anterior five-eighths of the sacral spine, deep to the origin of the M. gluteus maximus. The fibers aggregate to insert upon the anterior and proximal surfaces of the greater trochanter.

Innervation. N. gluteus superioris.

Action. Abductor and rotator of the femur; the anterior fibers would also flex the femur to some extent.

Discussion. If the M. gluteus minimus is represented in soricoids, it is fused with the M. gluteus medius; Leche identified a semi-independent, deeper part of this muscle mass as a M. gluteus minimus, but I could not so separate it.

M. femorococcygeus (gluteus longus) (figs. 16, 18).—In *Scapanus* and *Neürotrichus* this muscle originates by a flat aponeurosis from near the posterior end of the dorsal part of the lateral surface of the sacral spine. The flat muscle runs distally, parallel with the femur and the anterior edge of the M. biceps femoris, and inserts into the fascia covering the lateral surface of the shank; this fascia is attached to the falciform process and to the anterior crest of the tibia.

In *Sorex* the origin, course, and insertion of the muscle are as in *Scapanus* and *Neürotrichus;* it is, however, fused with the M. biceps femoris throughout its length and might be erroneously considered to be a part of the latter muscle were it not that the N. cutaneous femoris posticus emerges normally between the two muscles (fig. 16a) near their origins.

Action. Abductor of the hind limb and flexor of the shank.

Innervation. A branch from the peroneal portion of the sciatic nerve penetrates the medial surface of the muscle midway of its length.

M. tenuissimus (figs. 16, 18).—In *Scapanus* and *Neürotrichus* this flat, slender muscle originates from the dorsal aspect of the lateral surface of the sacral spine, immediately beneath the posterior half of the origin of the M. femorococcygeus and anterior to the origin of the M. semitendinosus II. The M. tenuissimus runs distally and posteriorly as a long band beneath the M. biceps femoris; it inserts upon the Achilles' tendon, deep to the part of the M. biceps femoris which inserts upon that tendon, but superficial to the insertions of the M. gastrocnemii and soleus upon the tendon.

In *Sorex* the muscle originates from the spine of the third sacral vertebra and does not run so far posteriorly as in *Scapanus* and *Neürotrichus;* the distal part of the muscle broadens and it inserts into the fascia of the lateral side of the shank, beneath the posterior part of the insertion of the M. biceps femoris into the same fascia.

Innervation. By a proximal branch from the peroneal part of the N. ischiadicus.

Action. Flexor of the shank; in *Scapanus* and *Neürotrichus* the muscle is also an extensor of the pes by reason of its insertion into Achilles' tendon.

Discussion. In *Condylura* the insertion is as in *Sorex* (Leche, 1883).

Postpelvic Components (Hip and Thigh)
Ventral Division (N. tibialis group)

M. obturator internus (figs. 16, 19).—In *Scapanus* the origin is from the medial surface of the anterior half of the horizontal ramus of the pubis; thus half of the origin lies along the ventral border of the obturator foramen and the other half lies anterior to the obturator foramen. The fibers of the thin, triangular muscle aggregate dorsally into a small, flat tendon which passes out of the pelvic cavity through the lesser (posterior) sciatic foramen and turns sharply laterad across the dorsal surface of the M. gemellus to insert upon the posteroproximal surface of the greater trochanter. In *Neürotrichus* and *Sorex* the muscle is similar except that the tendon of insertion passes dorsally through the lesser sciatic notch, which is the homologue of the lesser sciatic foramen of *Scapanus*.

Innervation. A tiny nerve from the sciatic plexus runs medially and follows the tendon of the muscle through the lesser sciatic foramen.

Action. Abductor and rotator of the femur.

Discussion. The M. obturator internus is merely a part of the M. gemellus which has migrated over the rim of the pelvis to reach its present location within the pelvic cavity (Howell, 1936b). In the soricoids the action of the muscle is strengthened by the insertion of some of the fibers of the gemellus into its tendon.

Dobson (1883) missed this muscle completely in the talpids, presumably because of its

small size and internal position. However, its fibers run at right angles to the axial muscles of the tail, which surround them, and with a little care they can be dissected out.

M. gemellus (figs. 16, 19).—In *Scapanus* the origins of the Mm. gemellus and quadratus femoris are fused, but the insertions are separate; one can follow back from the insertions and separate the two muscles. The origin of the M. gemellus is from the dorsolateral surface of the horizontal ramus of the ischium. The fibers aggregate anteriorly and slightly laterally to insert with the tendon of the M. obturator internus upon the posteroproximal portion of the greater trochanter.

In *Neürotrichus* the muscle is as described for *Scapanus* except that the origins of the Mm. gemellus and quadratus femoris are not fused.

In *Sorex* the Mm. gemellus, quadratus femoris, and the posterior part of the M. obturator externus are fused throughout and one can distinguish them only to the extent of correlating areas of origin and insertion with the same areas in *Scapanus*.

Action. The muscle is an abductor and rotator of the femur.

Discussion. Dobson (1883) failed to separate the M. gemellus from the M. quadratus femoris in all the talpids he dissected; he assigned the latter name to both muscles.

M. quadratus femoris (figs. 16-19).—In *Scapanus* this muscle originates from the horizontal ramus of the ischium, deep to the M. gemellus, and from the descending ramus of the pubis, deep to the origin of the M. semimembranosus. The fibers of the thick, triangular muscle aggregate anteriorly to insert upon the posterior surface of the lesser trochanter.

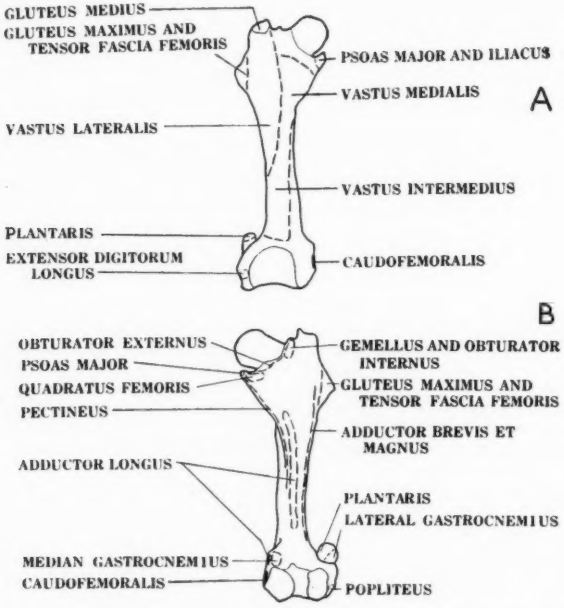

Fig. 19.—Femur of *Scapanus latimanus*, showing areas of muscle attachments, ×2.5. A. Anterior aspect. B. Posterior aspect.

In *Neürotrichus* the M. quadratus femoris lies completely posterior to the M. gemellus so that none of the former lies ventral to the latter. The two muscles are thus easily separated.

In *Sorex*, as discussed, the Mm. gemellus, quadratus femoris, and obturator externus cannot be separated.

Action. The muscle is a retractor and rotator of the femur; the rotatory action is in opposition to that of the M. gemellus.

Discussion. Dobson's (1883) failure to separate the Mm. gemellus and quadratus femoris has been mentioned.

M. biceps femoris (figs. 16, 18).—In *Scapanus* and *Neürotrichus* this muscle is the most superficial one which originates from the tuberosity of the ischium and the descending ramus of the pubis. The muscle runs distally, parallel with the femur, and widens slightly as it goes. Insertion of the anterior three-fourths of the muscle is into the lateral fascia of the shank in common with, but posterior to, the insertion of the M. femorococcygeus. The insertion of the posterior fourth of the M. biceps femoris is upon the Achilles' tendon.

Innervation. The proximal part of the muscle is innervated by a branch from the N. ischiadicus ventralis, the distal part by what I presume to be a normal sensory and motor nerve, although it comes off the N. cutaneous femoris posticus.

Action. Flexor of the shank; in part an extensor of the foot.

M. semimembranous (figs. 16-18, 21).—In *Scapanus, Neürotrichus,* and *Sorex* the origin of this muscle is from the dorsal two-thirds of the descending ramus of the pubis, deep to the origin of the M. biceps femoris. The muscle runs distally to insert upon the medial surface of the shaft of the tibia near the head of that bone. In *Scapanus* and *Sorex* the muscle inserts deep to the medial collateral ligament of the tibia; in *Neürotrichus* it inserts over this ligament and thus farther anteriorly upon the tibia.

Innervation. N. ischiadicus ventralis.

Action. Flexor of the shank.

M. semitendinosus.—In most mammals this muscle arises by two heads, one from the ischium and one from the sacrum and/or the caudal vertebrae. In soricoids these two heads are separate muscles and will be discussed as such, under the terminology as proposed by Leche (1883).

M. semitendinosus I (figs. 16-18, 21).—In *Scapnus, Neürotrichus,* and *Sorex* the origin of this muscle is from the ventral part of the descending ramus of the pubis, deep to the origin of the M. biceps femoris and superficial to the origin of the M. adductor brevis et magnus. The muscle runs distally to insert upon the anteromedial surface of the tibia posterior to the insertion of the M. semimembranosus. In *Neürotrichus* the insertion is upon the distal extension of the falciform process of the tibia and thus farther anterior than in the other two genera.

Innervation. N. ischiadicus ventralis.

Action. Flexor of the shank.

Discussion. Dobson's designation (1883) of this muscle as the M. gracilis is incorrect, inasmuch as the M. gracilis is innervated by the obturator nerve. Dobson's basic error was in assuming the presence of a M. sartorius, which confused his nomenclature throughout the medial side of the thigh.

M. semitendinosus II (figs. 16-18, 21).—In *Scapanus* and *Neürotrichus* the origin of this muscle is immediately posterior to that of the femorococcygeus, from the crest of the posterior eighth of the sacral spine and from the dorsal fascia and the spine of the first caudal vertebra; fibers of origin also spring from the transverse process of the first caudal vertebra. The muscle runs distally and curves around the posterior edge of the M. biceps femoris to become the most posterior muscle on the medial surface of the thigh. The muscle inserts in line with, but immediately behind and partly covered by, the insertion of the M. semitendinosus I.

In *Sorex* the origin of the muscle is broader, as it extends forward to the posterior

edge of the M. gluteus maximus on the spine of the third sacral vertebra. The insertion is almost entirely covered by the insertion of the M. semitendinosus II.

Innervation. N. ischiadicus ventralis.

Action. Flexor of the thigh.

Discussion. The factors in the soricoids responsible for the separation of the two heads of the M. semitendinosus into two distinct muscles are not known.

M. caudofemoralis (figs. 16-19).—In *Scapanus*, *Neürotrichus*, and *Sorex* this muscle originates by a short, narrow, flat tendon from the tuberosity of the ischium, deep to the

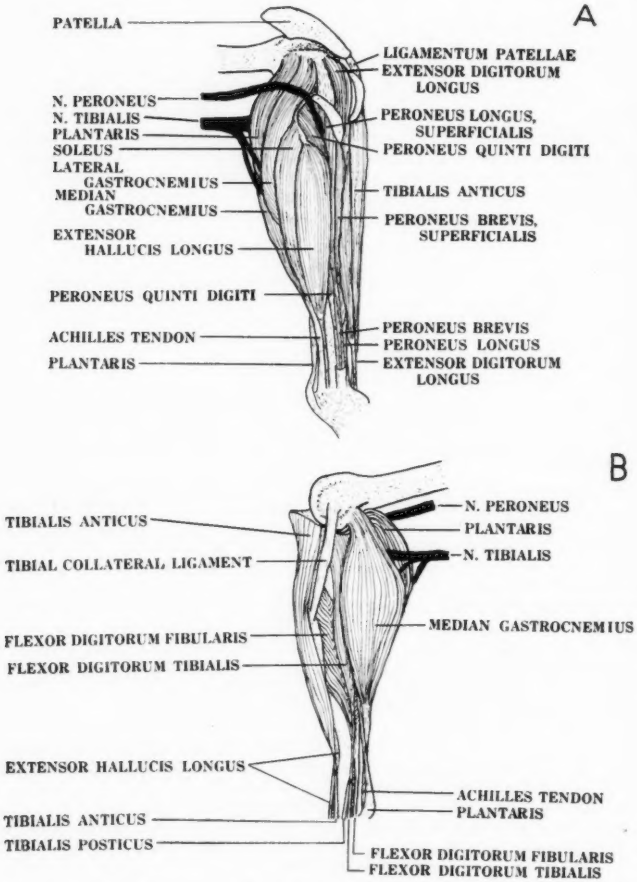

Fig. 20.—Shank musculature of *Scapanus latimanus*. A. Lateral aspect, ×2.5. B. Medial aspect, ×2.5.

dorsal part of the origin of the M. biceps femoris. The muscle broadens as it runs distally and slightly proximally to insert upon the medial epicondyle of the femur. In *Sorex* the insertion covers a wider area than in *Scapanus* or *Neürotrichus*.

Innervation. N. ischiadicus ventralis. Appleton (1928) did not discuss this muscle with those innervated by the N. ischiadicus ventralis, since he considered the muscle to be innervated by a separate branch from the N. tibialis. However, I was not able to separate the nerve to the M. caudofemoralis from the N. ischiadicus ventralis running to the hamstring muscle.

Action. Retractor of the femur.

Discussion. This muscle has probably been assigned more names by different investigators and been the subject of more phyletic speculation than has any other muscle in the thigh. Much of this confusion stems from Leche (1883), who named a M. caudofemoralis in the menotyphlous insectivores and a M. praesemimembranosus in the lipotyphlous insectivores; in the menotyphlous insectivores Leche thought that both of these muscles were present but that the M. praesemimembranosus was fused with the M. semimembranosus. Leche, usually so careful with his myological homologies, was actually dealing with but one muscle, the M. caudofemoralis, and calling it by two names; since the M. semimembranosus in the Menotyphla has no other muscle or part of a muscle fused with it, careful reading of Leche's paper will demonstrate that he claimed a M. praesemimembranosus in those genera in which a M. caudofemoralis is lacking, and *vice versa*. Appleton (1928) was the first to synonymize these two names and to clarify the situation.

Postpelvic Components (Crus and Pes)

Dorsal Division (N. peroneus group)

Anterior (N. peroneus profundus)

M. tibialis anticus (figs. 20-22).—In *Scapanus* this is a large muscle which originates from the anterior surface of the medial condyle of the tibia, from the depression in the anterior surface of the tibia distal to the condyle, from the distal border of the falciform process, from the lateral edge of the proximal sixth of the anterior surface of the shaft of the tibia, and from the anterior part of the lateral surface of the interosseous membrane between tibia and fibula. Immediately distal to the union of tibia and fibula the fibers converge into a strong tendon which runs down the anterior side of the crus and beneath the transverse crural ligament in company with the tendons of the Mm. extensor digitorum longus and extensor hallucis longus. The tendon then turns obliquely and medially across the tarsus to insert upon the medial surface of tarsale I midway of its length.

In *Neürotrichus* the origin is from the lateral rim of the falciform process, from the posterior surface of the proximal part of the falciform process, and from the connective tissue beneath the tip of the falciform process and the lateral process of the fibula. The course and insertion of the tendon are as in *Scapanus*.

In *Sorex* the M. tibialis anticus arises from the whole of the lateral surface of the falciform process and from the adjacent area of the tibial shaft. The insertion is more distal upon tarsale I than it is in *Scapanus*.

Action. Dorso-flexor and adductor of pes.

Discussion. In none of the specimens dissected by me was the origin from the fibula, as claimed by Dobson (1883) for part of the muscle in *Desmana* and *Condylura*, but in *Neürotrichus* part of the origin was from a connective tissue band attached to the fibula. The changes in origin of this muscle correlated with the changes in shape and position of the falciform process in the different genera have been mentioned in the discussion of the tibia-fibula (p. 577). Although one usually considers that variable muscular action and development is responsible for variable osseous characteristics in different genera, there do not seem to be any possible differences in the development and action of the M. tibialis anticus in these three genera to account for such extreme differences in the falciform process.

M. extensor digitorum longus (figs. 19, 20, 22).—In *Scapanus, Neürotrichus,* and *Sorex* the origin is from the anterior surface of the lateral epicodyle of the femur. The muscle runs deep to (*in Sorex* lateral to) the falciform process and continues down the anterolateral side of the crus; at the distal end of the crus the fibers aggregate into a tendon which immediately separates into four parts. These tendons pass beneath the transverse crural ligament and a more distal transverse ligament; they then separate, one tendon going to each of the four lateral digits. Each tendon divides dorsoventrally at the distal end of the metatarsal; the deep tendon is inserted upon the dorsal surface of the first phalanx, the superficial tendon is inserted upon the distal phalanx. For the fourth and fifth digits there are collateral tendons of insertion which merge diffusely with the interdigital connective tissue.

Action. General extensor and adductor of digits II, III, IV, and V; dorso-flexor of the foot upon the crus.

M. extensor hallucis longus (figs. 20-22).—In *Scapanus, Neürotrichus,* and *Sorex* this muscle arises from a small area on the posterolateral side of the tibia above the junction of that bone and the fibula and from the adjacent interosseous membrane. The area of origin does not show on drawings of muscular attachments of the tibia-fibula. The small muscle extends almost the length of the shank; the round tendon passes beneath the transverse crural ligament between the tendons of the Mm. extensor digitorum longus and tibialis anticus and then passes beneath a transverse ligament of its own (not shown in fig. 22). In *Scapanus* and *Neürotrichus* the tendon runs diagonally and medially across the foot to insert upon the sesamoid dorsal to the joint at the distal end of metatarsal I. From this sesamoid a tendon continues to the dorsoproximal surface of the distal phalanx of the hallux.

In *Sorex* the tendon of this muscle divides into three parts, distributed to digits I, II, and III, of which the one to the hallux is the smallest. Each tendon runs out the lateral side of its respective digit, is attached to the proximal end of the first phalanx, and continues to insert on the proximal end of the second phalanx.

Action. In *Scapanus* and *Neürotrichus* the muscle is an extensor and adductor of the hallux; in *Sorex* it is an extensor of digits I-III and an adductor of digits I and II.

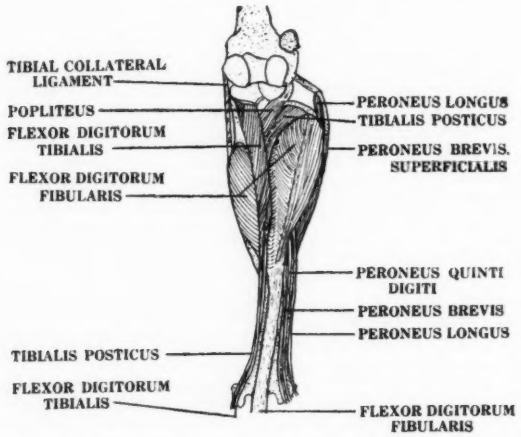

Fig. 20C.—Shank musculature of *Scapanus latimanus,* posterior aspect, after removal of the Mm. gastrocnemii, soleus, and plantaris, ×2.5.

POSTPELVIC COMPONENTS (Crus and Pes)
DORSAL DIVISION (N. peroneus group)
LATERAL (N. peroneus superficialis)

M. peroneus longus (figs. 20-25).—In *Scapanus* and *Neürotrichus* this muscle arises by two heads, a superficial head from the posterior surface of the lateral process of the fibula, and a deep head from the tibial surface beneath the lateral condyle of the tibia. The two heads join at the level of the junction of fibula and tibia; the fibers almost immediately form a tendon which passes distally and through the more lateral of the two canals on the posterior surface of the lateral malleolus. The tendon passes plantad to the lateral process of the calcaneus, through a groove in the distal end of tarsale IV + V (cuboid), and obliquely and medially across the pes. In *Scapanus* it inserts into the lateroproximal angle of metatarsal I. In *Neürotrichus* the tendon divides; the more proximal inserts as in *Scapanus*, but the more distal broadens into a muscle, the median of the three Mm. flexores breves to digit II.

In *Sorex* the peroneus longus originates from the anterior rim of the head of the fibula. The course of the muscle is as in *Scapanus*. At the distal end of the tarsus the

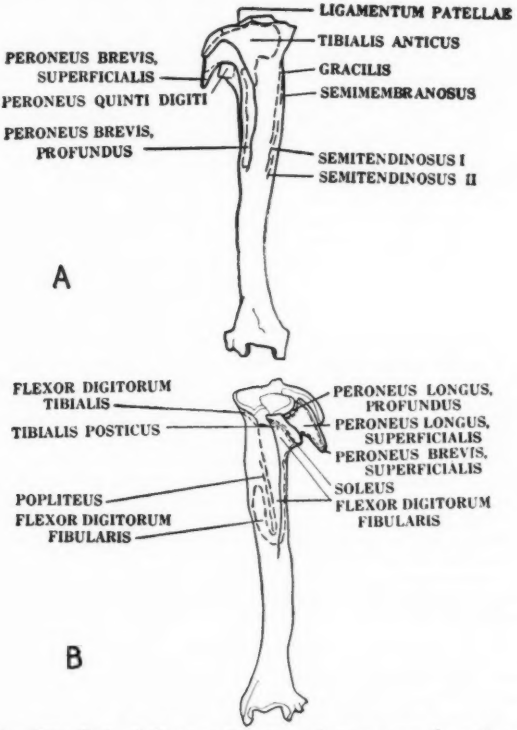

Fig. 21.—Tibia-fibula of *Scapanus latimanus*, showing areas of muscle attachments, ×2.5. A. Anterior aspect. B. Posterior aspect.

tendon divides into two parts; of these the lateral inserts upon the proximal end of metatarsal V. The medial tendon runs obliquely and medially across the planta and divides into four tendons. Of these, the most proximal inserts upon the lateroproximal angle of metatarsal I; the remaining three tendons expand into muscular bellies which serve as the two Mm. flexores breves to digit II and the medial M. flexor brevis to digit III.

Action. In all three genera the muscle is an adductor of digit I; this action, if continued, would move all digits laterally with reference to the tarsus. The function of the tendon of insertion upon metatarsal V in *Sorex* is not understood. The tendons to some of the Mm. flexores breves in *Neürotrichus* and *Sorex* probably do not flex the digits but merely serve as points of origin for those muscles.

M. peroneus brevis (figs. 20-22).—In *Scapanus* and *Neürotrichus* the muscle originates by two heads, a superficial head from the distolateral part of the anterior surface of the lateral process of the fibula, and a deep head from the anterior surface of the fibular shaft between the neck of the lateral process of the fibula and the point of junction of fibula and tibia, and from the lateral surface of the interosseous membrane adjoining the fibula. The two heads join below the union of fibula and tibia; the tendon is sturdy and continues down the posterolateral side of the crus, passes behind the lateral malleolus in company with the Mm. peroneus digiti quinti and peroneus digiti quarti (the latter lacking in *Scapanus*), crosses dorsally to the lateral process of the calcaneus, and then curves around the lateral edge of tarsale IV + V (cuboid). Midway of the calcaneus the tendon gives off a slender slip which merges with the interdigital connective tissue of digits II and III. The main tendon inserts upon a lateral tubercle which projects from the proximal end of metatarsal V.

In *Sorex* the M. peroneus brevis originates from the anteromedial surface of the proximal fibular shaft, from beneath the anterior projection of the head of the fibula, by a strong tendon from the anterior surface of the lateral condyle of the tibia, and from the proximal portion of the anterolateral surface of the shaft of the tibia. The course and insertion of the muscle are as in *Scapanus*.

Action. The muscle is an abductor of digit V; this action, if continued, would move all of the digits laterally with reference to the tarsus.

M. peroneus digiti quinti (M. peroneus digiti V; Straus, 1930) (figs. 20-22).—In *Scapanus* and *Neürotrichus* the muscle originates from the anterolateral side of the posterior process of the fibula and from the shaft of the fibula a short distance distally. In *Sorex* the muscle originates from the lateral surface of an anterior extension of the head of the fibula. In all three genera the small muscle runs down the lateral side of the crus and gives rise to a slender tendon which passes posterior to the lateral malleolus in company with the Mm. peroneus brevis and peroneus digiti quarti (the latter missing in *Scapanus*). The tendon emerges upon the dorsolateral surface of the pes and proceeds down the dorsolateral side of digit V to insert upon the proximal end of the second phalanx.

Action. The muscle is an abductor of digit V.

M. peroneus digiti quarti (M. peroneus digiti IV; Straus, 1930).—In *Neürotrichus* and *Sorex* this muscle originates from the lateral and anterolateral surfaces of the shaft of the fibula, immediately distal to the head of the fibula. The tendon accompanies that of the M. peroneus digiti quinti, but proceeds down the dorsolateral side of digit IV to insert on the proximal end of the second phalanx in *Neürotrichus* and upon the proximal end of the distal phalanx in *Sorex*. In *Sorex* there is a cross-connective between the tendon of the M. peroneus digiti quarti and the tendon of the M. extensor digitorum longus to digit III; this connective holds each tendon parallel with its respective digit so that each will act solely as an extensor.

Action. In *Neürotrichus* an extensor and abductor of digit IV, in *Sorex* an extensor of digit IV.

Discussion. Dobson (1883) described this muscle in *Desmana* and *Condylura*, but found it absent in *Scapanus*, *Talpa*, and *Scalopus*. The M. peroneus digiti quarti must not be confused with the human M. peroneus quartus, which is actually a rudimentary M. peroneus digiti quinti inserting on the calcaneum or the cuboid (Straus, 1930; Gray's Anatomy, twenty-third edition, p. 483).

POSTPELVIC COMPONENTS (Crus and Pes)

VENTRAL DIVISION (N. tibialis group)

Mm. gastrocnemii (figs. 19, 20).—In *Scapanus, Neürotrichus,* and *Sorex* the origin of the M. gastrocnemius lateralis is from the distal half of the posterior side of the sesamoid on the lateral supracondyloid ridge of the femur; the origin is fused for a short distance with the origin of the M. plantaris. The M. gastrocnemius medialis originates from the posterior side of the medial epicondyle of the femur. Both are large, flat-bellied muscles which become tendinous midway of the length of the shank. The two tendons fuse to form the tendon of Achilles, which inserts upon the calcar of the fibulare.

Action. Extensor of the pes.

M. soleus (figs. 20, 21).—In *Neürotrichus* and *Scapanus* this short muscle originates from the proximal edge of the medial surface of the posterior process of the fibula and by a weak tendon from the lateral side of the origin of the lateral head of the M. gastrocnemius. The insertion is into the proximal part of the tendon of Achilles. In *Sorex* the muscle originates on the most posterior part of the rim of the head of the fibula and by superficial connective tissue from the proximal part of the lateral side of the lateral head of the M. gastrocnemius; insertion is by a distal fusion with the lateral head of the M. gastrocnemius.

Action. Ventro-flexor of the pes.

Discussion. Dobson (1883: 156) described a tibial head of origin from the falciform process in *Desmana;* no trace of any such origin was found in *Sorex, Neürotrichus,* or *Scapanus.* Dobson's figure of *Desmana* (plate 16) shows the origin of the M. soleus from the lateral epicondyle of the femur in company with the lateral head of the M. gastrocnemius; this drawing is presumably erroneous in this respect.

M. plantaris (figs. 19, 20, 22).—In *Scapanus, Neürotrichus,* and *Sorex* the muscle originates from the proximal half of the posterior surface of the sesamoid bone upon the lateral supracondyloid ridge of the femur. The muscle is large but laterally compressed between the two Mm. gastrocnemii. Midway of the crus the muscle becomes tendinous; this tendon lies deep to the tendon of Achilles, but curves medially around it to lie upon it and then broadens to continue distally over the calcaneus. From this broad part of the tendon, fascial sheets extend medially to the medial tarsale and laterally to the lateral malleolus of the tibia-fibula. The main tendon continues distally upon the planta and divides into three tendons, which insert upon digits II, III, and IV.

In *Scapanus* the tendon to digit IV crosses superficially to the large tendon of the M. flexor digitorum fibularis to digit IV and then divides into three tendons. Two of these attach to the two sesamoids at the distal end of metatarsal IV, the other of these three tendons continues distally, deep to the tendon of the M. flexor digitorum fibulris, to insert upon the proximal end of phalanx 2. The tendon to digit III passes distally, medial to the tendon to the same digit from the M. flexor digitorum fibularis, and divides into three tendons at the level of the distal end of metatarsal III. The most lateral and the weakest of these passes deep to the tendon of the M. flexor digitorum fibularis, to insert upon the lateral side of the distal end of the distal phalanx. The central tendon to digit III passes distally, covered by the tendon of the M. flexor digitorum fibularis, to insert upon the proximal end of phalanx 2. The medial tendon inserts on the proximomedial edge of the distal phalanx of digit III. The tendon to digit II inserts as does the tendon to digit III.

In *Neürotrichus* the insertion of the three tendons of the M. plantaris is as in *Scapanus* except for some minor, and seemingly unimportant, differences of arrangements of sesamoids.

In Sorex there are three main tendons of insertion, one each to digits II, III, and IV, as in the talpid genera; each of these three divides into three lesser tendons, the middle one of which is the strongest. This middle tendon on each digit runs medially and then deep to the tendon of the M. flexor digitorum fibularis and inserts on the seamoid at the proximal end of the second phalanx; the medial tendon of each group of three fuses with the tendon of the M. flexor digitorum fibularis to that digit, and the lateral tendon merges with the interdigital connective tissue.

Action. The muscle is a flexor of the toes; this action, if continued, will result in ventro-flexion of the pes.

M. flexor digitorum fibularis (figs. 20-22).—In *Scapanus* this muscle originates by two heads, although these heads are fused throughout their length and are difficult to separate. The lateral head originates from the medial surface of the posterior process of the fibula distal to the areas of origin of the Mm. soleus and tibialis posticus, and from the postero-medial surface of the shaft of the fibula. The medial head originates from most of the medial surface of the interosseous membrane between fibula and tibia, from most of the posterolateral surface of the shaft of the tibia proximal to the junction of tibia and fibula

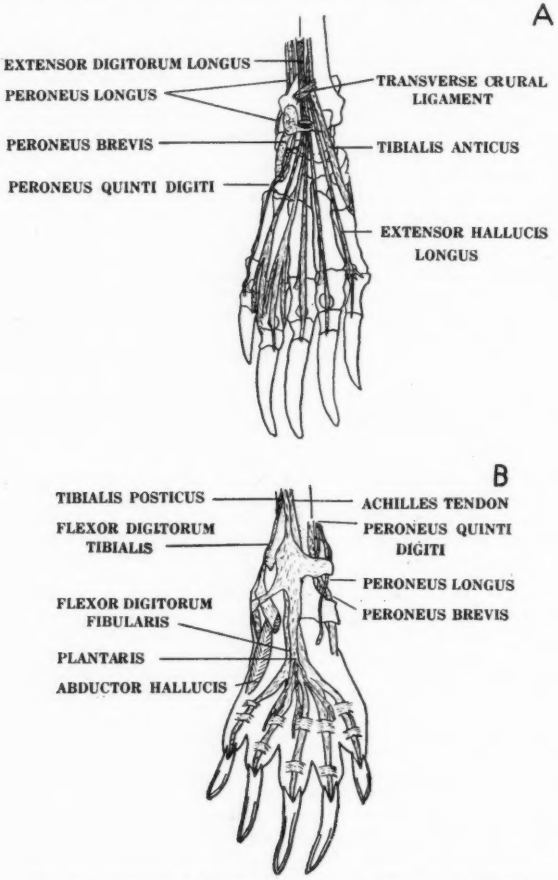

Fig. 22.—Tendons of the pes of *Scapanus latimanus*. A. Dorsal aspect, ×2.5. B. Plantar aspect, ×2.5.

and posterior to the line of attachment of the interosseous membrane, from the postero-lateral rim of the medial condyle of the tibia, and from the central third of the postero-medial surface of the shaft of the tibia medial to the line of insertion of the M. popliteus. Upon the posterior surface of the medial head, the Mm. flexor digitorum tibialis and tibialis posticus lie in a deep groove. Distal to the point of union of tibia and fibula the two heads of the M. flexor digitorum fibularis continue into a straight broad heavy tendon which passes across the posterior surface of the ankle-joint medial to the calcaneus and onto the planta, where it is covered by the tendon of the M. plantaris. At the proximal end of the metatarsals the single tendon divides into five tendons, one of which continues out each digit to insert upon the distal end of the distal phalanx.

In *Neürotrichus* the insertion of the muscle is as in *Scapnus*, but the origin differs in that the two bipinnate heads are separate and that the lateral head consists only of the fibers which originate from the posterior process of the fibula. A tendon from each head runs down the posterior surface of the shank; these unite at the level of the calcaneus.

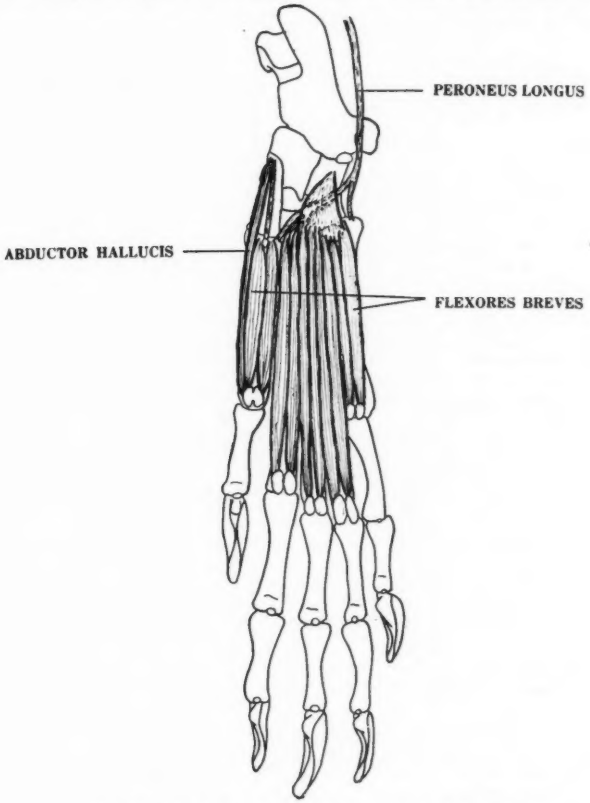

Fig. 23. Muscles of the pes of *Sorex trowbridgii*, ×8.6.

In *Sorex* the muscle also arises by two heads; the lateral and smaller of these arises from the proximal portion of the posterolateral surface of the shaft of the fibula. The medial head is as in *Scapanus* except that it lacks the part which originates from the shaft of the tibia medial to the insertion of the M. popliteus. The two tendons of these two heads unite and insert as in *Neürotrichus*, except that the insertion is complicated by the relationships with the tendons of insertion of the M. flexor digitorum tibialis (which see).

Action. Flexor of the five digits and ventro-flexor of the pes.

Discussion. This muscle is the homologue of the human M. flexor hallucis longus, and sometimes is ssigned that name in comparative anatomical studies. In many mammals, however, as in the soricoids, the tendons of insertion are not limited to the hallux, and the retention of the name "hallucis" is confusing; Schulze (1866) proposed the name here used to avoid this confusion and this name has generally been adopted by comparative anatomists.

M. flexor digitorum tibialis (figs. 20-22).—In *Scapanus* this muscle originates from

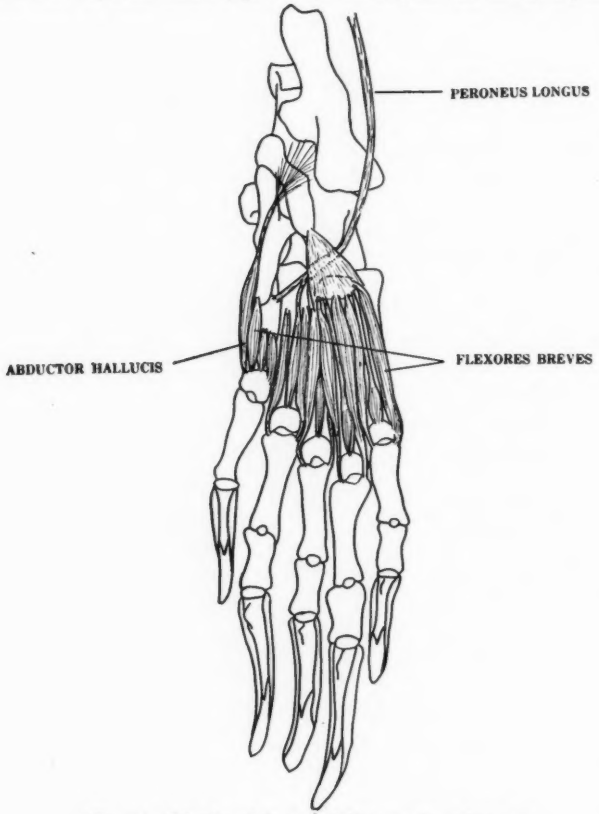

Fig. 24.—Muscles of the pes of *Neürotrichus gibbsii*, ×8.

the posteriomedial surface of the medial condyle of the tibia. The muscle is small, fusiform, and lies with the M. tibialis posticus in a groove on the posterior surface of the medial head of the M. flexor digitorum fibularis. The long tendon extends half the length of the crus and passes through the groove on the posterior side of the medial malleolus. The tendon broadens over the medial surface of the proximal planta and is attached by its medial side to the medial tarsale; since there is a ligament between the medial tarsale and the medioproximal edge of metacarpal I, contraction of the muscle results in tension on the ligament and abduction of the hallux. The main part of the tendon continues past the medial tarsale to insert into the dermal pad on the medial side of the sole. Contraction of the muscle would pull this dermal pad medioposteriorly.

In *Neürotrichus* the muscle differs from that in *Scapanus* only in that it inserts completely into the medial tarsale. There is a tendon, as in *Scapanus,* from the medial tarsale to metatarsal I.

In *Sorex* the origin and course of this muscle are as in *Scapanus;* at the proximal end of the tarsus the tendon divides into two. Of these, the medial one inserts into the medial tarsale, but there is no ligament continuing to metatarsal I, only loose connective tissue. The lateral tendon is small and fuses to the plantar surface of the tendon of insertion of the M. flexor digitorum fibularis and accompanies the four medial tendons of that muscle to their insertions.

Action. In *Scapanus* the muscle abducts the hallux and broadens the sole of the foot; it thus aids the pes in gaining a firm grip upon the substrate. In *Neürotrichus* the muscle abducts the hallux. In *Sorex* the muscle is a flexor of digits I-IV.

Discussion. This muscle is the homologue of the M. flexor digitorum longus of man, where it is the main flexor of digits II-V. In many mammals, as in the talpids, the number of insertions is reduced and the muscle becomes small and unimportant. Schulze (1866) proposed the name here used to avoid the confusion inherent in the use of the human name; his nomenclature has generally been used by comparative anatomists.

M. tibialis posticus (figs. 20-22).—In *Scapanus* and *Neürotrichus* the origin is from the anterior half of the proximal rim of the medial surface of the posterior process of the fibula, deep to the origin of the M. soleus. This small short muscle has a long weak tendon which passes in company with the tendon of the M. flexor digitorum tibialis through the groove in the posterior surface of the medial malleolus. In three *Scapanus* specimens the tendon inserted into the proximal tip of the centrale, in one specimen it inserted into the proximal tip of tarsale I. In four specimens of *Neürotrichus* insertion was into tarsale I.

In *Sorex* the muscle arises from the medial surface of the head of the fibula. The muscle is short; the small tendon is completely enveloped in a closed groove on the posterior surface of the M. flexor digitorum fibularis but its course is as in *Scapanus.* The tendon inserts as in *Neürotrichus,* after it has spiraled around a ligament which extends from the anterior surface of the medial malleolus to the plantar surface of the proximal end of tarsale I.

Action. The muscle pulls the pes medially and would tend to extend it; however, the extremely small size of the muscle indicates a feeble action.

M. popliteus (figs. 19-21).—In *Scapanus* and *Neürotrichus* the muscle originates from a small depression on the distal surface of the lateral epicondyle of the femur, runs medially and distally across the posterior surface of the knee joint, and inserts on the middle half of the posterior crest (popliteal line) of the tibia. In *Sorex* the muscle originates from the sesamoid which lies between the lateral epicondyle of the femur and the head of the fibula, but its course and insertion are as in *Scapanus.*

Action. Although the muscle is theoretically a flexor of the shank upon the thigh and a rotator of the shank at the knee-joint, it probably serves best to strengthen the knee-joint against a force which would rotate the lateral side of the shank posteriorly.

Mm. flexores breves (Mm. interossei) (figs. 23-25).—In *Sorex* there are ten of these deep short flexors, two to a digit; in *Neürotrichus* there are fifteen of these muscles, three to a digit. It is not thought that descriptions of these muscles are necessary, since a drawing of this group of muscles is presented in detail for each genus (figs. 23-25). Only the

origins of the middle and lateral muscles for digit III of *Neürotrichus* could not be shown; the origin of the former is in two parts, a medial head from the medial surface of the proximal end of metatarsal III, and a lateral head by a long tendon from the medial side of the proximal end of metatarsal IV. The muscle on the lateral side of digit III of *Neürotrichus* originates by a tendon from the same point on metatarsal IV as does the lateral head of the middle muscle to the same digit.

The three Mm. flexores breves to the hallux of *Neürotrichus* are completely tendinous or have so few muscle fibers that they could have little function; the remainder of the muscles, however, are muscular throughout or have small distal muscular bellies. In *Sorex* all are muscular throughout.

Presumably two Mm. flexores breves to a digit is the basic mammalian condition (McMurrick, 1907); the factors responsible for the realignment of muscle fibers to form three to a digit in *Neürotrichus* are not known. The muscles in *Neürotrichus* show a tendency toward degeneration, as compared with *Sorex*, both with regard to the paucity of muscular fibers in some of them and with regard to the distal migration of the origins with a consequent shortening of the muscle.

In *Neürotrichus* one of the Mm. flexores breves takes origin from the tendon of insertion of the M. peroneus longus; in *Sorex* three of the muscles take origin from this tendon. Probably the origins of the muscles shifted to the tendon rather than the tendon subdividing and sending extensions distally to becomes muscles.

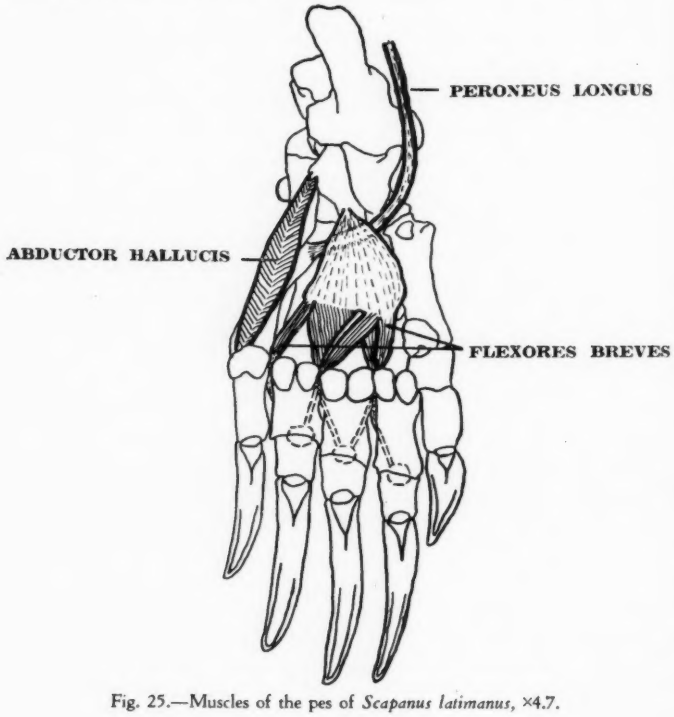

Fig. 25.—Muscles of the pes of *Scapanus latimanus*, ×4.7.

In *Scapanus* the Mm. flexores breves are reduced to five tiny bundles, two each for digits II and III and the medial flexor for digit IV. As in *Neürotrichus*, the muscles are so extremely small that it does not seem possible they can have any functional significance. In *Scapanus* each of the surviving Mm. flexores breves takes origin, at least in part, from a broad tarsal ligament which is also present in *Sorex* and *Neürotrichus*, but in these latter genera it serves as origin for only part of the Mm. flexores breves. In *Scapanus* the small distal tendons of the four lateral muscles spiral around the digit to insert on the dorsal surface upon a sesamoid at the distal end of the first phalanx (fig. 23); the muscles in the other two genera do not insert upon the dorsal surface of the pes. Insertion in all genera is at the proximal end of the first digit, either directly or through intervening sesamoids.

The trend toward degenercy of the Mm. flexores breves with an increase in fossorial life is not understood. In every other character studied the more fossorial animals possess adaptations for general strengthening of the hind limb and for broadening and strengthening of the pes; the latter adaptations are to be correlated with the necessity for a broader foot and a firmer grip upon the substrate when burrowing. The condition of the Mm. flexores breves, however, would seem to reverse that trend, as what one would consider to be a useful set of muscles for the hind foot of a burrowing animal is undergoing degeneration. It is possible that the shortening manifest in the metatarsals of *Neürotrichus* and *Scapanus*, particularly the latter, mechanically inhibits the development of the Mm. flexores breves.

M. abducor hallucis (figs. 23-25).—This small muscle runs from an origin on the tarsus to the medial side of the sesamoid at the distal end of metatarsal I; the muscle was present in every specimen of each genus dissected. Its homology and correct name remain unknown, so that the name here given is one of convenience only. Unlike the Mm. flexores breves, this muscle increases in size with increase in fossorial activity; by abduction of the hallux it serves a useful function for a fossoril animal because of the consequent broadening of the foot.

SUMMARY OF THE MUSCULATURE OF THE HIND LIMB

The musculature of the soricoid hind limb is not specialized and requires little discussion. The primary adaptations for a fossorial life would seem to be in the skeleton, but in general the crural flexors insert more distally upon the crus in *Scapanus* than in *Neürotrichus* or *Sorex* and the muscles of the crus are heavier and shorter in *Scapanus* than in *Neürotrichus* or *Sorex*. Both of these conditions in *Scapanus* are correlated with the shorter crus, which is an adaptation for a fossorial life (p. 580).

The Mm. sartorius and pyriformis are lacking in all soricoids dissected by me; among the insectivores the M. sartorius supposedly occurs only in *Tupaia* and *Erinaceus* (Leche, 1883: 85), and the M. pyriformis supposedly is found only in menotyphlous insectivores (Leche, 1883: 75).

The M. semitendinosus has been found to be separated into two muscles in *Crocidura* and talpine moles (Leche, 1883: 90), *Desmana* and *Condylura* (Dobson, 1883), *Talpa* (Appleton, 1928), and in *Sorex*, *Neürotrichus*, and *Scapanus*. The Mm. femorococcygeus and biceps femoris were fused in *Sorex*, but not in the other genera dissected.

The M. peroneus digiti quarti was found in *Sorex* and *Neürotrichus* but not in *Scapanus;* it has also been described in *Crocidura* (Ärnbäck-Christie-Linde, 1907) and in *Desmana* and *Condylura* (Dobson, 1883).

In *Sorex*, *Neürotrichus*, and *Scapanus* all intrinsic musculature of the pes is lacking except for a M. abductor hallucis and the Mm. flexores breves; the

latter are increasingly degenerate in the more fossorial genera, but the M. abductor hallucis is more robust in the fossorial forms. In *Crocidura* (Ärnbäck-Christie-Linde, 1907) the Mm. extensor digitorum brevis, flexor digitorum brevis, and flexor accessorius are present, and in *Desmana* (Dobson, 1883: 156) a M. adductor minimi digiti is present, in addition to the Mm. flexores breves.

Without evidence as to the relative sizes of the functional groups of muscles within the hind limb, no attempt can be made to correlate the differences in use of these muscular groups with differences in locomotion.

THE FORE LIMB

BRANCHIOMERIC MUSCULATURE

M. trapezius.—The trapezius is the only branchiomeric muscle considered in the present paper, as it is the only one playing a direct part in locomotion. The trapezius is divided into two muscles in *Sorex* and *Scapanus*, into three in *Neürotrichus*. These muscles will be considered separately.

M. trapezius anticus (figs. 26, 29).—In *Sorex* the muscle originates in two parts, a smaller part from the parietal-occipital suture immediately lateral to the dorsal midline, and the larger from the raphe of the dorsal midline, between the posterior end of the occipital bone and the first thoracic vertebra. The muscle runs laterally and ventrally to insert on the lateral surface of the metacromion; the insertion is covered by the insertion of the M. atlanto-scapularis anterior.

In *Neürotrichus* the muscle also originates in two parts, but both are on the dorsal midline. The first part originates from the occiput, the second from the nuchal ligament. The muscle inserts as in *Sorex*, except that it must run forward and ventral to the metacromion, due to the forward migration of the anterior end of the scapula.

In *Scapanus* the muscle is degenerate; a connective tissue band between the occipital midline and the acromion, with a few muscular fibers contained within it, is probably the homologue of the M. trapezius anticus.

Innervation. N. spinal accessory (cranial XI).

Action. In *Sorex* the muscle can pull the anterior end of the scapula dorsally and slightly anteriorly, or it can shift the whole scapula dorsally. In *Neürotrichus* the muscle can only pull the anterior end of the scapula dorsally and slightly posteriorly. In *Scapanus* there is no action.

Discussion. The function of the muscle is to shift the position of the head of the scapula, and consequently of the shoulder-joint. In *Scapanus* the clavicle is extremely short and is capable of anteroposterior motion only. Since the clavicle has a joint with the humerus, the position of the shoulder-joint is immobilized; with the lack of any possible action, the muscle has degenerated in *Scapanus*, as it has in all Talpinae (Campbell, 1939). Dobson (1883: 166) described the muscle correctly in *Condylura* but erroneously assumed its presence in the talpine moles. Edwards (1937) and Freeman (1886) failed to realize the absence of this muscle in *Scalopus* and *Talpa* and assigned its name to the M. rhomboideus capitis, which is the most superficial scapular muscle in the talpines.

M. trapezius medius (figs. 26, 29).—This tiny muscle was found by me only in *Neürotrichus*, but it would seem to have been described by Dobson (1883: 150) as the M. transversus scapularum in *Desmana*, where it is larger and shows somewhat different relationships. In *Neürotrichus* it is small, flat, and thin and originates from the extreme posterior end of the nuchal ligament. It runs laterally, superficial to the Mm. rhomboideus capitis and rhomboideus cervicis, to insert into the tuberosity of the scapular spine immediately anterior to the insertion of the M. trapezius posticus.

Innervation. N. spinal accessory (cranial XI), which passes beneath the muscle and sends a tiny twig into its ventral surface.

Action. The action of the muscles of the two sides would be to pull the posterior ends of the scapulae together, except that such small muscles could hardly be effective.

Discussion. Dobson (1883) thought the M. transversus scapularum in *Desmana* to be a part of the rhomboideus complex, but the M. trapezius medius in *Neürotrichus* is clearly a member of the accessory field. The phylogenetic origin of this muscle is not clear, as it is absent in most soricoids. It could be either an undifferentiated, degenerating, intermediate remnant of an originally continuous M. trapezius or it could be a part of the M. trapezius anticus whose origin had remained stable but whose insertion had shifted posteriorly along the spine of the scapula.

M. trapezius posticus (figs. 26, 29).—This muscle is similar in all three genera studied; it is long, flat, slim, originates from the lumbar neural spines and lombodorsal fascia, and runs forward to insert on the tuberosity of the scapular spine. In *Sorex* it originates from the third and fourth lumbar vertebrae, in *Neürotrichus* from the third to sixth lumbar vertebrae, and in *Scapanus* from the second and third lumbar vertebrae. In *Neürotrichus* the posterior fibers originate in common with some of the fibers of the M. latissimus dorsi, but in the other two genera the two muscles are completely separate.

Innervation. N. spinal accessory (cranial XI).

Action. In *Sorex* contraction of the muscle will pull the dorsal (vertebral) border of the scapula posteriorly; in *Neürotrichus* the entire scapula will be pulled posteriorly and held braced; in *Scapanus* the bracing action alone is possible, since the head of the scapula is held firmly at its anterior surface by the nature of the shoulder-joint and the scapula cannot move posteriorly.

MYOMERIC MUSCULATURE

DORSAL DIVISION

M. splenius.—This epaxial muscle must be mentioned briefly, since in *Scapanus* it originates upon the nuchal ligament ventral to the Mm. rhomboidei and inserts on the occipital bone; there is a similar slip in *Neürotrichus*. Primarily the muscle serves to turn and elevate the head, but it may secondarily brace the nuchal ligament and thus steady the origin of the M. rhomboideus cervicis. In *Neürotrichus* there is an additional latero-posterior slip, which originates from the anterior portion of the middorsal raphe of the M. rhomboideus posticus; this second slip of the M. splenius runs forward, lateral to the first slip, to insert with it. The failure to recognize the lack of a M. trapezius anticus in *Scalopus* led Edwards (1937) to misapply names to all subsequent muscle layers in this region, so that he included the M. splenius, as here described, with the rhomboideus group.

M. serratus posterior superior.—This epaxial muscle must also be included in a discussion of soricoid limb myology because of its intimate relationship to the M. rhomboideus posticus.

Although the origin of this muscle in most mammals is from the vertebral spines of the thoracic vertebrae, in *Sorex* the origin has separated from the vertebrae dorsally and is from the muscle of the other side by a median raphe, immediately deep to the origin of the posterior part of the M. rhomboideus posticus; the two muscles are difficult to separate at their origins. The M. serratus posterior superior runs laterally, ventrally, and posteriorly, deep to the M. serratus anterior thoracis, and inserts into the osseocartilaginous junctions of the third and fourth ribs.

In *Neürotrichus* the origin is similar to that in *Sorex*, but the insertion is upon the third rib only. In *Scapanus* the muscle consists of two stout slips which originate from the anterior face of the median portion of the interscapular ligament of the M. rhomboideus posticus and run anterolaterally to insert upon the third and fourth ribs immediately lateral to the long epaxial musculature of the back.

Innervation. The innervation of this small muscle was not determined, so it has not been definitely proved to be an epaxial muscle.

Action. In *Sorex* and *Neürotrichus* the muscle could serve to elevate the ribs or to tighten and thus brace the median raphe from which the M. rhomboideus posticus takes origin. In *Scapanus* the muscle may either elevate the ribs or tighten the interscapular ligament.

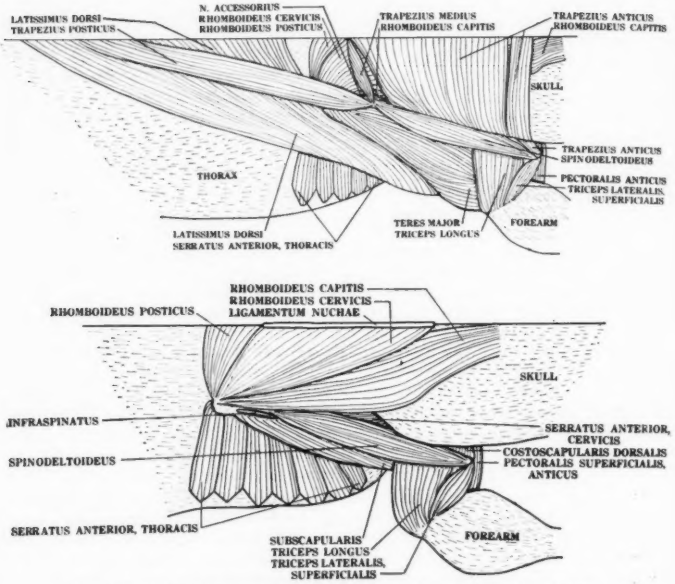

Fig. 26.—Shoulder musculature of *Neürotrichus gibbsii*, dorsal view. A. Superficial layer, ×3.5. B. Deeper layer, ×3.7.

Discussion. The primary function of the M. serratus posterior superior in most mammals is to assist in respiration by raising the ribs upon which it inserts. In soricoids, however, the muscle has become associated with the M. rhomboideus posticus and assists that muscle by bracing its point of origin. In the talpines the muscle has shifted its origin from the dorsal midline to the interscapular ligament, which is merely a part of the M. rhomboideus posticus, in order to brace that muscle more securely in the more fossorial genera.

Dobson (1883) considered this muscle to be a part of the M. rhomboideus posticus, an error corrected by Freeman (1886).

Myomeric Musculature

Lateroventral division—Appendicular system (pectoral limb)

Dorsal (extensor) Division

Dorsoscapular (suprazonal) Group

These are myomeric muscles between the axial skeleton and the scapula.

M. rhomboideus capitis (figs. 26, 29).—In all three genera the muscle originates from the parieto-occipital suture, immediately lateral to the midline of the skull. The muscle is thin and flat, and converges posteriorly and somewhat laterally to insert on the vertebral border of the scapula deep to the insertion of the M. rhomboideus cervicis.

Innervation. From branches of the cervical plexus; these were not identified exactly.

Action. In *Sorex* the muscle would pull the vertebral border of the scapula anteriorly; in *Neürotrichus* and *Scapanus* the tendency would be toward the same action, but the scapula is more firmly fixed in these talpids and the action would be less apparent.

M. rhomboideus cervicis (figs. 26, 29).—In all three genera the muscle originates from the nuchal ligament, beneath the origin of the M. trapezius anticus (absent in *Scapanus*). The fibers of the muscle, which is flat and thin at its origin, converge posteriorly and laterally to insert into the vertebral border of the scapula superficially to the insertion of the M. rhomboideus capitis.

Innervation. Cervical nerves II, III, and IV.

Action. The muscle will pull the vertebral border of the scapula anteromedially and dorsally, and thus act against the Mm. teres major and serratus anterior thoracis, which pull the scapula ventrally and laterally.

Discussion. Owen (1868: 17) named the Mm. rhomboideus cervicis and rhomboideus capitis the M. trapezius; presumably he was discussing *Talpa* and did not note the absence of the M. trapezius anticus.

M. rhomboideus posticus (figs. 26, 29).—This muscle has undergone extensive

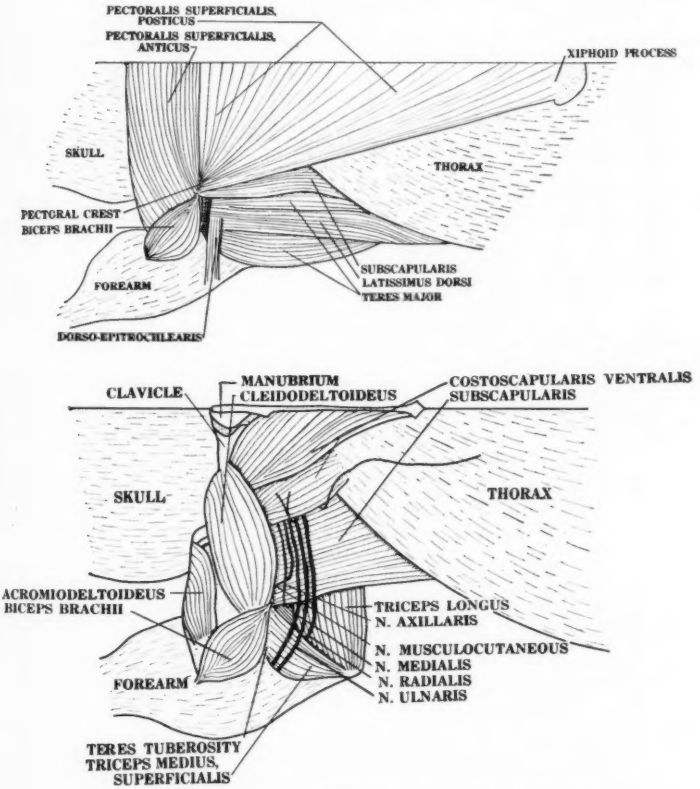

Fig. 27.—Shoulder musculature of *Neürotrichus gibbsii*, ventral view. A. Superficial layer, ×4. B. Deeper layer, ×5.

TABLE 36.—Muscles of the shoulder and brachium

Ärnbäck-Christie-Linde, *Crocidura*	Dobson, *Desmana*	Dobson, *Condylura*	Freeman, *Talpa*	Campbell, Soricoidea	Edwards, *Scalopus*	Reed, Soricoidea
1. Trapezius anticus	Trapezius anticus + occipito-scapularis externus	Trapezius anticus	(Overlooked)	Trapezius anticus	(Overlooked)	Trapezius anticus
2. (Not present)	Transversus scapularum (?)	(Not present)	(Not present)	(Overlooked?)	(Not present)	Trapezius medius
3. Trapezius posticus	Trapezius posticus	Trapezius posticus	Posterior trapezius	Posterior trapezius	Posterior trapezius	Trapezius posticus
4. Occipital part, rhomboideus anticus	Occipital part, rhomboideus anticus	Occipital part, rhomboideus anticus	Anterior trapezius	Rhomboideus capitis	Anterior trapezius	Rhomboideus capitis
5. Cervical part, rhomboideus anticus	Cervical part, rhomboideus anticus	Cervical part, rhomboideus anticus	Rhomboideus	Rhomboideus cervicis	Cervical part, rhomboideus anterior	Rhomboideus cervicis
6. Rhomboideus posticus	Postero-external part, rhomboideus posticus	Postero-external part, rhomboideus posticus	Interscapular ligament + dorso-interscapularis	Rhomboideus thoracis and/or interscapularis, and/or interscapular ligament	Rhomboideus posterior	Rhomboideus posticus
7. Splenius	Splenius capitis	(Undescribed)	(Undescribed)	(Undescribed)	Occipital part, rhomboideus anterior	Splenius
8. Levator anguli scapulae	Levator angulae scapulae	Levator angulae scapulae	Levator anguli scapulae	Serratus anterior cervicis	Levator scapulae	Serratus anterior cervicis
9. Levator scapulae	Levator scapulae vel claviculae	"Not represented"	(Undescribed)	Atlanto-scapularis anterior	(Undescribed)	Atlanto-scapularis anterior
10. (Undescribed)	(Undescribed)	(Undescribed)	(Undescribed)	Atlanto-scapularis posterior	(Undescribed)	Atlanto-scapularis posterior
11. Serratus anticus	Serratus magnus	Serratus magnus	Serratus magnus	Serratus anterior thoracis	Serratus anterior (magnus)	Serratus anterior thoracis
12. Pars superior, serratus [illegible]	Antero-external part, rhomboideus posticus	Antero-external part, rhomboideus posticus	Serratus posticus superior	Serratus posterior superior	(Undescribed)	Serratus posterior superior
[illegible] ficial pectoralis	[illegible] pectoralis major	[illegible] pectoralis major	[illegible] slips 3 and 4	[illegible] pectoralis superficialis	[illegible]	[illegible] anticus
14. Posterior superficial	Sternal part, pectoralis major	Sternal part, pectoralis major	Pectoralis major, slips 1, 2, 6 and 7	Pars sternalis, pectoralis superficialis	Posterior superficialis pectoralis	Pectoralis superficialis posticus

11. Serratus anticus	Serratus magnus	Serratus magnus	Serratus magnus	Serratus anterior thoracis	Serratus anterior (magnus)	Serratus anterior posterior
12. Pars superior, serratus posticus	Antero-external part, rhomboideus posticus	Antero-external part, rhomboideus posticus	Serratus posticus superior	Serratus posterior superior	(Undescribed)	Serratus anterior thoracis
[illegible] ficial pectoralis	pectoralis major	pectoralis major	slips 3 and 4	pectoralis superficialis	[illegible] pectoralis	Serratus posterior superior anticus
14. Posterior superficial pectoralis	Sternal part, pectoralis major	Sternal part, pectoralis major	Pectoralis major, slips 1, 2, 6 and 7	Pars sternalis, pectoralis superficialis	Posterior superficialis pectoralis	Pectoralis superficialis posticus
15. Deep pectoralis	(Undescribed)	Pectoralis minor	Pectoralis major, slip 5	Pectoralis profundus	Posterior deep pectoralis	Pectoralis profundus
16. (Not present)	Sterno-clavicularis	(Overlooked?)	Subclavius	Subclavius	Pectoralis minor and Subclavius	Costoscapularis ventralis
17.	Sterno-scapulatus					Costoscapularis dorsalis
18. Subclavius	Subclavius (?)	Subclavius	(Overlooked)	(Overlooked)	(Overlooked)	Subclavius
19. Latissimus dorsi	Latissimus dorsi	Latissimus dorsi	Latissimus dorsi	Latissimus dorsi	Latissimus dorsi	Latissimus dorsi
20. Teres major	Teres major	Teres major	Teres major	Teres major	Teres major	Teres major
21. Dorso-epitrochlearis	Dorso-epitrochlearis	Dorso-epitrochlearis	Dorso-epitrochlearis	Dorso-epitrochlearis	Tensor fascia antibrachii	Dorso-epitrochlearis
22. Clavicular part, deltoideus	Clavicular part, pectoralis major	Clavicular part, pectoralis major			Anterior deep pectoralis major	Cleido-deltoideus
23. Acromial part, deltoideus		Deltoideus	Deltoid	Cleido-deltoid	Deltoid	Acromio-deltoideus
24. Scapular part, deltoideus	Deltoideus	Infraspinatus	Infraspinatus	Spino-deltoid (Teres minor)	Teres minor	Spinodeltoideus
25. Infraspinatus	Infraspinatus		(Not present)	Infraspinatus	Infraspinatus	Infraspinatus
26. Supraspinatus	Supraspinatus	Supraspinatus	Supraspinatus	Supraspinatus	Supraspinatus	Supraspinatus
27. (Not mentioned)	Teres minor	"Missing"	"Entirely absent"	(Not mentioned)	(Not mentioned)	Part of subscapularis (?)
28. Subscapularis	Subscapularis	Subscapularis	Subscapularis	Subscapularis	Subscapularis	Subscapularis
29. Anconeus	Triceps	Triceps	Triceps	Triceps brachii	Triceps brachii	Triceps brachii
30. Brachialis anticus	Brachialis anticus	Brachialis anticus	Brachialis anticus	Brachialis	Brachialis	Brachialis
31. Biceps brachii	Biceps	Biceps	Biceps brachii	Biceps brachii	Biceps brachii	Biceps brachii
32. (Not mentioned)	(Not mentioned)	Anconeus externus	Anconeus	(Not mentioned)	Anconeus externus	Anconeus externus

changes within the soricoids and has therefore been given a variety of names by different investigators. Campbell (1939) alone seems to have grasped the evolutionary history of the muscle, but he confused the issue again by discussing the one muscle under three different names in different soricoids.

In *Sorex* the muscle is flat, weak, and originates anteriorly from the posterior end of the nuchal ligament and posteriorly from the same muscle of the other side by a middorsal raphe. The muscle narrows laterally to insert upon the ventral edge of the axillovertebral angle of the scapula. In *Blarina* (Campbell, 1939, M. rhomboideus thoracis) and in *Crocidura* (Arnbäck-Christie-Linde, 1907) the muscle originates from neural spines and not from a middorsal raphe.

In *Neürotrichus* the muscle has no vertebral connection but originates only from a median raphe marking the line of fusion with the same muscle of the other side. The insertion is upon the vertebral border of the scapula, covered by the common insertion of the Mm. rhomboideus capitis and rhomboideus cervicis. The condition in *Urotrichus* is similar or identical (Campbell, 1939). When the muscle continues across from scapula to scapula without origin from vertebral spines, as in *Neürotrichus*, Campbell terms it an "interscapularis," although his Mm. rhomboideus thoracis and interscapularis are obviously one and the same muscle in different genera.

In *Condylura* (Campbell, 1939) a part of the muscle, only, has lost its vertebral origin and gained middorsal origin on its antimere; in this circumstance Campbell applies different names to the two parts of the same muscle. In *Galemys* (Campbell, 1939) the muscle is also in two parts, but both have lost their vertebral origin and run from scapula to scapula; *Galemys* thus has two "interscapular muscles," according to Campbell.

The condition of the muscle in *Scapanus* may have been derived from a type such as is found in *Condylura;* in *Scapanus* it is divided into two parts, one of which is entirely ligamentous (the "interscapular ligament" of Campbell). The ligamentous portion runs across the back between the vertebral borders of the scapulae. The muscular part originates from the neural spines of the third and fourth thoracic vertebrae, runs posteriorly, ventral to the M. serratus anterior thoracis, and then turns around the posterior edge of that muscle to insert into the distal half of the ligamentous portion (interscapular ligament). The two antimeres, although originating from the vertebral spines, are somewhat fused at their origins. *Scalopus, Parascalops, Talpa,* and *Mogera* have a M. rhomboideus posticus of the same type as does *Scapanus* (Campbell, 1939).

Innervation. N. dorsalis scapulae from cervical nerve V.

Action. In all soricoids the action of the muscle is to draw the vertebral end of the scapula dorsally and medially and to brace it against forces acting to separate the scapulae.

Discussion. The changes in morphology of this muscle can be correlated closely with the locomotor habits of most genera. In *Crocidura* and *Blarina* the condition is simple; the muscle runs from the neural spines to the vertebral border of the scapula. *Neürotrichus, Urotrichus,* and *Galemys,* all of which are semi-fossorial, have a muscular band from scapula to scapula, but are without osseous origin; *Sorex,* curiously enough, has the same type of muscle. *Condylura,* which is more fossorial than the other Desmaninae but less so than the talpines, has retained a part of the muscle attached to the vertebral column but a part stretches across the dorsum between the scapulae; both parts, however, are muscular. In the talpines, and only in them, the interscapular part has become ligamentous, and the muscular part serves to tighten this tendon. With increased fossorial activity there would seem to be a greater need to brace the vertebral ends of the scapulae so that they are held firmly together. Probably the M. serratus anterior thoracis acts against the interscapular ligament to hold the vertebral end of the scapula firmly in place; the M. teres major acts against the interscapular ligament to displace the vertebral ends of the scapulae laterally.

Campbell's mixed terminology led him into the confusion of stating that *Blarina* has a M. rhomboideus thoracis but no interscapularis, that *Neürotrichus* has a M. interscapularis but no rhomobideus thoracis, that *Condylura* has both interscapularis and rhomboideus thoracis, and the talpines have an interscapular ligament and a rhom-

boideus thoracis. This confusion is unnecessary if we regard these different arrangements merely as variants of a single muscle which may separate into two slips, one of which may become completely tendinous.

The relationship of the M. serratus posterior superior to the M. rhomboideus posticus in all genera dissected has been discussed (p. 617).

The muscle was not saved in *Scapanus* for volumetric mensuration because of the difficulty of removing it cleanly at its points of origin.

M. serratus anterior thoracis (figs. 26, 29).—In *Sorex* the muscle arises by five slips from the osseo-cartilaginous junctions of the anterior five ribs. The slips converge to insert upon the median side of the axillovertebral angle of the scapula. In *Blarina* (Campbell, 1939) the condition is similar; in *Crocidura* (Ärnbäck-Christie-Linde, 1907) there are nine slips from the first nine ribs.

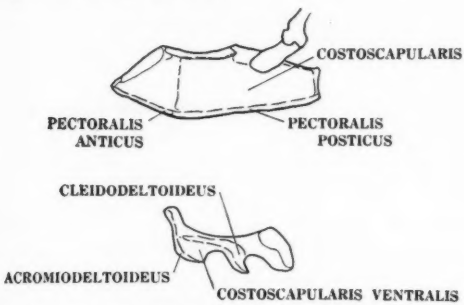

Fig. 28.—Manubrium and clavicle of *Neürotrichus gibbsii*, showing areas of muscle attachments, ×5.

In *Neürotrichus* the muscle originates by seven slips, from the third to the ninth ribs, inclusively. The insertion is upon the median surface of the vertebral border of the scapula. In *Desmana* (Dobson, 1883: 150) there are eight slips, from the second to the ninth ribs, inclusively; in *Condylura* (Dobson, 1883: 167) there are also eight slips, from the first eight ribs.

In *Scapanus* the muscle originates by eight slips, from the third to the tenth ribs, inclusively. The insertion lies beneath that of the interscapular ligament on the vertebral border of the scapula.

Innervation. N. longus thoracicus.

Action. In *Sorex* the muscle will pull the vertebral end of the scapula anteriorly and ventrally; in the talpids it would pull the vertebral end of the scapula ventrally if it were not for the restraining action of the M. rhomboideus posticus (or the interscapular ligament derived from that muscle). In the talpids, therefore, the M. serratus anterior thoracis serves to fix the scapula; also it supports the body between the limbs.

M. serratus anterior cervicis (figs. 26, 29).—In *Sorex* there are six slips, of which the first is the largest and originates from the wing of the atlas immediately lateral to the origin of the M. atlanto-scapularis anterior. The other slips spring from the transverse processes of the remaining cervical vertebrae, except that none could be found from the axis.

All of the slips converge posteriorly to insert upon the medial edge of the anterior half of the vertebral border of the scapula. In *Crocidura* (Ärnbäck-Christie-Linde, 1907) the muscle originates only from the fourth to the sixth cervical vertebrae.

In *Neürotrichus* the origin is by a series of fused slips from the transverse processes of the third to seventh cervical vertebrae, from the tuberculum of the first rib, and by a separate slip from the osseo-cartilaginous junction of the first rib. The insertion is upon the medial side of the axillovertebral angle of the scapula.

In *Scapanus* the muscle originates by conjoined slips from the transverse processes of the last four cervical and the first two thoracic vertebrae. Insertion is as in *Neürotrichus*.

Innervation. By branches from the cervical plexus; the exact nerves involved were not determined.

Action. In *Sorex* the muscle will pull the vertebral end of the scapula anteriorly; in *Neürotrichus* and *Scapanus* the scapula lies nearly parallel with the direction of the muscle, so that the action is an anterior movement of the whole scapula. In *Neürotrichus* a certain amount of such motion is possible, due to the relatively long clavicle, but in *Scapanus* this movement is extremely limited, and the action would be limited accordingly to a forward thrust against the head of the humerus and the clavicle. In addition, the muscle will

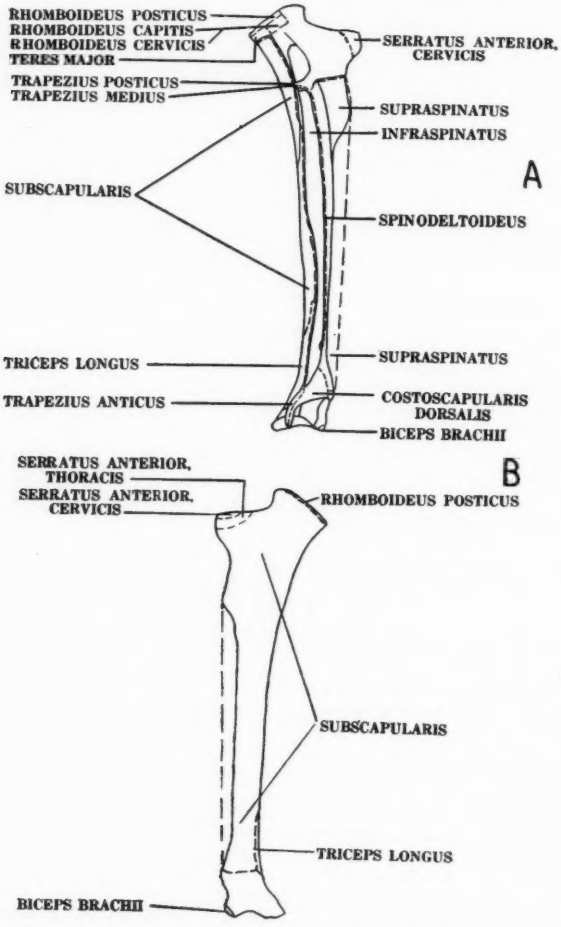

Fig. 29.—Scapula of *Neürotrichus gibbsii*, showing areas of muscle attachments. A. Dorsolateral aspect, ×5. B. Ventromedial aspect, ×5.

coöperate with the Mm. trapezei, rhomboidei, and the serratus anterior thoracis in fixation of the scapula.

Discussion. If one accepts the descriptions of the various authors writing on soricoid shoulder anatomy, one must conclude that the areas of origin of this muscle in different genera are extremely variable. However, the cervical region of a soricoid is difficult to dissect and errors are easily made, so that I suspect some of the literature is unreliable. The muscle was not saved for volumetric calculations in my dissections because of the difficulty of removing it cleanly at its points of origin.

M. atlanto-scapularis posterior.—Among the soricoids this muscle has been reported only from *Blarina* (Campbell, 1939); it was not found in any of the three principal genera dissected by me, but was found in *Blarina*. It is a flat, straplike muscle which originates from the transverse process of the atlas immediately posterior to the origin of the M. atlanto-scapularis anterior. From its origin the muscle runs first laterally around the epaxial musculature and then posteriodorsally to insert upon the ridge of the dorsal end of the scapular spine. The posterior part of the muscle lies in contact with, but lateral to, the M. rhomboideus capitis.

Innervation. Not determined.

Action. The muscle pulls the vertebral end of the scapula anteriorly and ventrally.

Discussion. The muscle is presumably a part of the M. serratus anterior cervicis whose insertion has moved onto the scapular spine. Its phylogenetic history among the soricoids must remain unknown until more shrews have been dissected.

M. atlanto-scapularis anterior.—In *Sorex* this is a narrow, flat muscle which originates on the anteroventral edge of the wing of the atlas near its base. The muscle curves around the lateral edge of the M. splenius and inserts on the distal tip of the metacromion, superficial to the insertion of the M. trapezius anticus.

The muscle is absent in *Neürotrichus* and *Scapanus*, but has been described in *Desmana* (Dobson, 1883: 150), in *Blarina* (Campbell, 1939), and in *Crocidura* (Ärnbäck-Christie-Linde, 1907).

Innervation. Not determined.

Action. In *Sorex* the muscle would draw the anterior end of the scapula forward and somewhat medially.

Discussion. The muscle is supposedly derived by an anterior migration down the scapular spine of a slip of the M. serratus anterior cervicis. Its absence in *Neürotrichus*, *Condylura*, and all the talpines ever described indicates its loss of function with the reduced mobility of the shoulder-joint, which is in turn associated with a more fossorial life.

DORSAL (EXTENSOR) DIVISION, SHOULDER GROUP, THORACODORSAL MATRIX

These are myomeric muscles between the axial skeleton and the humerus, or muscles derived from this primary group.

M. latissimus dorsi (figs. 26, 27, 30, 31).—In *Sorex* this muscle originates from the posterior thoracic and anterior lumbar vertebrae, from the lumbodorsal fascia, and from the dorsal ends of the posterior ribs. The fibers aggregate anteriorly and ventrally to insert on the teres tubercle, superficial to the insertion of the M. teres major; the insertion is not fused with the insertion of that muscle. The M. latissimus dorsi is similar in *Blarina* (Campbell, 1939) and *Crocidura* (Ärnbäck-Christie-Linde, 1907).

In *Neürotrichus* this is a broad, strong muscle which originates on the most posterior thoracic and all of the lumbar neural spines, but not from the sacrum or ilium. The muscle runs anteriorly and ventrally over the lateral surface of the enlarged M. teres major and fuses with that muscle just posterior to their common insertion upon the teres tubercle.

In *Scapanus* the origin is from the neural spines of the posterior four thoracic vertebrae, from all the lumbar vertebrae, and from the lumbodorsal fascia extending over the iliac crest and the anterior end of the sacral spine. It courses and inserts as in *Neürotrichus*.

Innervation. N. thoracodorsalis.

Action. The muscle is a retractor and rotator of the humerus, and as such is an important muscle in fossorial activity (p. 658).

Discussion. The more extensive origin of the M. latissimus dorsi in *Scapanus* as compared with *Neürotrichus* is probably correlated with the more fossorial life of *Scapanus*. There is no tendency toward a deep and a superficial division of the muscle as found in *Talpa* and *Mogera* (Campbell, 1939).

M. teres major (figs. 26, 27, 29-31).—In *Sorex* and *Neürotrichus* this muscle originates from the lateral surface of the axillo-vertebral angle of the scapula, runs anteroventrally, and inserts upon the teres tubercle deep to the insertion of the M. latissimus dorsi. The muscle is far larger in *Neürotrichus* than in *Sorex*, and in *Scapanus* it has become tremendously hypertrophied until it is the largest muscle in the body; in *Scapanus* it has a greater area of origin than in *Neürotrichus* inasmuch as it originates from the whole of the teres fossa and from a part of the vertebral border. In *Neürotrichus* and *Scapanus* the muscle fuses with the M. latissimus dorsi before their common insertion upon the teres tubercle.

Innervation. Cervical nerves VI and VII, by the N. axillaris.

Action. This is a powerful retractor and rotator of the humerus, and as such is the most important of those muscles inserting on the humerus which are used in the digging stroke.

Discussion. The great increase in size of this muscle with increase in fossorial life is indicative of its use in the digging stroke. In *Scapanus* the M. teres major is fused for a greater distance with the M. latissimus dorsi than in *Neürotrichus*. In both *Neürotrichus* and *Scapanus* the lateroventral edge of the muscle along the axillary border of the scapula is fused with the adjoining edge of the M. subscapularis. In *Scapanus* the M. teres major does not originate in part from the interscapular ligament, as reported for *Talpa* by Freeman (1886).

The statement by Freeman (1886) that Owen (1868: 17-18) had confused the Mm. teres major and deltoid is an error by Freeman. Owen's "deltoid" is my spinodeltoideus; this muscle and the M. teres major are both figured and described accurately by Owen.

SHOULDER GROUP

AXILLARY MATRIX

Primitively this was a single sheet originating from the membranous girdle; with the disappearance of the cleithrum a portion of the sheet settled upon the scapula to form the M. teres minor, another portion arose from the clavicle to become the M. deltoideus; the M. subscapularis may also be derived from this group (Howell, 1937b).

M. teres minor.—As Campbell (1939) pointed out, there is no way of knowing whether the M. teres minor is or is not represented in the soricoids, as the muscle I am calling the M. spinodeltoideus may well be the M. teres minor. Both lie on the lateral side of the scapula, insert on the greater tuberosity, and are innervated by the N. axillaris. If one is absent, as it is in the soricoids, there is no way of knowing which one it is. However, I prefer to reserve the name "teres minor" for the mammalian muscle which originates upon the axillary border of the scapula between th Mm. infraspinatus and teres major; no such muscle occurs in any soricoid dissected, and so I am adopting the point of view that the M. teres minor is absent. Campbell (1939) and Edwards (1937) use the name "teres minor" for the muscle I am designating as the M. spinodeltoideus, and are perfectly justified in doing so.

Dobson's (1883: 152) use of the term "teres minor" is another situation, as he obviously described a separate head of the M. subscapularis as the "teres minor" and even described its insertion on the greater tuberosity, where a M. teres minor would insert, instead of on the lesser tuberosity, where his drawing (pl. 17) shows it inserting and where the M. subscapularis does insert. There is such a separate head of the M. subscapularis in

Galemys (Campbell, 1939) and in *Neürotrichus;* presumably the same is true for *Desmana.*

M. spinodeltoideus (figs. 26, 29, 30).—In *Sorex* this is a strong, spindle-shaped muscle, overlying in part the Mm. infraspinatus and teres major. The origin is from the dorsal half of the posterior side of the scapular spine and from the surface of the posterior part of the vertebral border. The muscle narrows to run beneath the metacromion and inserts onto the posterior side of the distal two-thirds of the deltoid ridge.

In *Neürotrichus* the muscle is longer than in *Sorex,* in correlation with the lengthening of the scapula. It is a strong muscle which originates from the tuberosity of the scapula and the length of the crest of the scapular spine. The muscle runs beneath the metacromion to insert upon the small deltoid ridge, which in this genus appears merely as a spine on the greater tuberosity.

In *Scapanus* the muscle is stout, covers the Mm. infraspinatus and supraspinatus, and is fused in part with them. Origin, course, and insertion are as in *Neürotrichus;* the tendon of insertion passes lateroventrally to the acromion.

Innervation. N. axillaris.

Action. The muscle is a retractor and counter-rotator of the humerus; that is, the rotatory action is in opposition to that of the Mm. teres major, latissimus dorsi, subscapularis, and pectoralis superficialis posticus.

M. acromiodeltoideus (figs. 27, 28, 31).—In *Sorex,* as in *Crocidura* (Ärnbäck-Christie-Linde, 1907), this is a short triangular muscle which covers the lateral side of the greater tuberosity. It originates from the ventral surface of the distal half of the acromion and the acromioclavicular joint, and the fibers converge to insert with the M. cleidodeltoideus into the lateral side of the distal tip of the pectoral process (and not into the deltoid ridge, as claimed by Ärnbäck-Christie-Linde for *Crocidura*). In *Sorex* the muscle is a weak abductor of the humerus.

In *Neürotrichus* the origin of the muscle has shifted entirely to the clavicle, where it is attached to the anteroventral angle of the distal end. The muscle runs over the greater tuberosity and around the lateral side of the humerus to insert into the disal end of the pectoral ridge. The muscle has the same function as in *Sorex,* but the humerus projects laterally, so that the muscle elevates the humerus.

In *Scapanus* the muscle is much as in *Neürotrichus* except that the origin has shifted to the median end of the anterior side of the clavicle and the insertion does not quite reach the distal end of the pectoral ridge. The muscle has the same action; since, however, the talpine humerus projects dorsolaterally, contraction of the muscle will draw the true lateral edge of the humerus toward the back of the animal.

Innervation. N. axillaris.

M. cleidodeltoideus (figs. 27, 28, 31).—In *Sorex* this is a short triangular muscle lying medial to, but in contact with, the M. acromiodeltoideus; it originates from the posterior surface of the distal fifth of the clavicle, covers the anterior aspect of the greater tuberosity, and the fibers converge to insert with the M. acromiodeltoideus onto the lateral side of the distal tip of the pectoral ridge (not into the deltoid ridge, as claimed by Ärnbäck-Christie-Linde, 1907, for *Crocidura*). The muscle is a weak adductor of the humerus; together with the M. acromiodeltoideus it will extend the humerus anteriorly.

In *Neürotrichus* this is a short, comparatively heavy muscle, which originates on the ventral surface of the lateral half of the clavicle; it is closely connected to the cleidohumeral joint-capsule and inserts into the proximal portion of the pectoral ridge (as separated from the pectoral crest) of the pectoral process.

In *Scapanus* the muscle is similar to that in *Neürotrichus,* except that it takes origin from a tubercle on the ventral surface of the clavicle and inserts more broadly upon the pectoral ridge. It is adjacent to, but separate from, the M. acromiodeltoideus.

In the talpids it is also an adductor of the humerus, as it is in *Sorex,* but since the humerus extends laterally or dorsolaterally the muscle acts as a depressor and thus in *Scapanus* it will swing the distal end of the humerus away from the body.

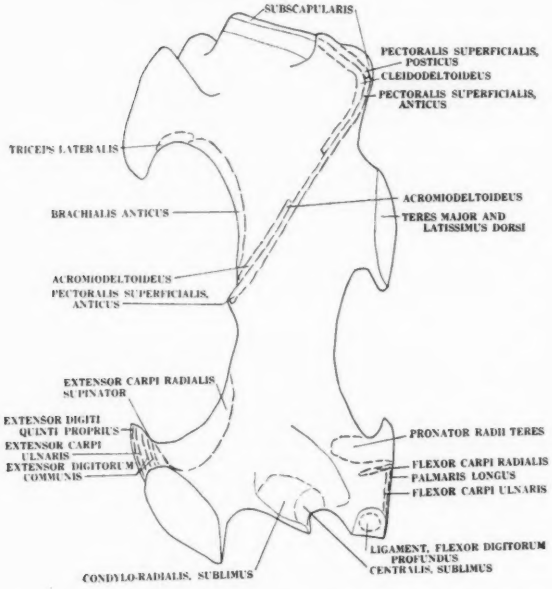

Fig. 30.—Humerus of *Neürotrichus gibbsii*, anterior view, showing areas of muscle attachments, ×12.4.

Innervation. N. axillaris.

Discussion. The deltoids are one of the most interesting muscle groups in the soricoids, and one of the least understood by previous investigators. Campbell failed to stress the fundamental division of the Mm. cleidodeltoideus and acromiodeltoideus into two separate entities, although in *Condylura*, by his own statement, the division is complete. One must begin with a shrew, however, as we have, and realize that there are two muscles which are adjacent but which can be separated; one lies to the lateral side of the long axis of the humerus and is an abductor (M. acromiodeltoideus), and the other lies to the medial side of the long axis of the humerus and is an adductor (M. cleidodeltoideus). In *Neürotrichus* and *Scapanus* the M. acromiodeltoideus has shifted along the acromioclavicular ligament to the clavicle, but the fundamental plan of action of both muscles is maintained; with the growth of the pectoral process in the talpids, and the crossing of the pectoral ridge from the medial to the lateral sides of the humerus, the abductor inserts on the lateral side and remains as an abductor, the adductor inserts on the medial side and remains as an adductor. In *Sorex*, by acting together, the two muscles will extend the humerus anteriorly; in the talpids they may retain this possibility of action.

Howell (1937b) stated that the origin of the M. deltoideus was primitively limited to the clavicle and that it later migrated to the scapula in part or in whole. If this be true, we have in the soricoids an interesting example of reversal of evolution, for the M. acromiodeltoideus has migrated from the acromion back onto the clavicle.

Apart from having traced the Mm. acromiodeltoideus and cleidodeltoideus through a phylogenetic series from the condition in *Sorex* to that in *Scapanus*, the axillary innerva-

tion of both muscles in all genera justifies their inclusion within the deltoid group, a fact recognized previously by Freeman (1886) and Campbell (1939).

The confusion by various authors of the M. spinodeltoideus in whole or in part with the M. infraspinatus will be treated under the discussion of the latter muscle (p. 639).

M. subscapularis (figs. 26-28, 30, 31).—Howell (1936b) tentatively placed the M. subscapularis with the thoracodorsal matrix of the shoulder group of the extensor muscles, but later (1937b) he placed it tentatively with the axillary group. The proper classification of this muscle is therefore not possible at present, and I will here follow his more recent conclusions.

In *Sorex* the muscle is divided into two parts, the smaller of which lies next to the M. teres major but cannot be a part of that muscle because the axillary nerve runs between them. The origin of the larger head is from the entire surface of the subscapular fossa; that of the smaller head is from the axillary border of the scapula. The two parts of the muscle narrow abruptly; the larger inserts upon the proximal tip of the lesser tuberosity, the smaller inserts immediately adjacent and distal to it.

In *Neürotrichus* the origin is again in the same two parts; in addition the larger part projects dorsally beyond the coracoid border and originates from an intermuscular septum which it has in common with the M. supraspinatus. The M. subscapularis runs parallel with, but medially to, the M. teres major; the two heads of the M. subscapularis fuse and the single muscle inserts upon the whole of the proximal surface of the lesser tuberosity.

In *Scapanus* the muscle differs from the foregoing in that a division into two heads is not noticeable and that its area of origin on the axillary border has been lost to the M. teres major, thus restricting the origin of the M. subscapularis to the subscapular fossa and to the intermuscular septum it has in common with the M. supraspinatus.

Innervation. From cervical nerves VI and VII by subscapular nerves, usually three in number.

Action. In all three of the genera dissected the muscle is a rotator of the humerus coöperating with the Mm. teres major, latissimus dorsi, and the posterior fibers of the pectoralis superficialis posticus. The flexing action of the M. subscapularis would be slight or nil, even in *Sorex*, due to the extremely proximal point of insertion; in the talpids the point of insertion is more proximal than either the head or the greater tuberosity of the humerus, and thus the muscle may be able to act as an extensor.

Discussion. Howell's uncertainty as to the phylogeny of this muscle has been mentioned. In addition he believed (1937b) that the posterior part is homologous with the reptilian subscapular, but that the anterior part has been derived from the M. supraspinatus. The two heads observed here in *Sorex* and *Neürotrichus* would have nothing to do, however, with such a dual origin. The two-headed origin was not observed in *Crocidura* (Ärnbäck-Christie-Linde, 1907), but is present in *Galemys*, whereas in *Condylura* the origin is single, but the insertion double (Campbell, 1939).

Dobson's confusion of the smaller head of the M. subscapularis in *Desmana* with an imaginary M. teres minor has already been noted (p. 626).

SHOULDER GROUP, ELBOW MATRIX, BRACHIAL DIVISION

The elbow matrix of the extensor musculature consists of those muscles which bridged the elbow-joint in primitive tetrapods; of these some have moved their origins proximally and become more efficient extensors of the antebrachium. These latter constitute the brachial division of the elbow musculature (Howell, 1937b).

M. triceps brachii (figs. 29-34).—The M. triceps is divided into three heads (long, lateral, and medial) which may in turn be subdivided. In *Sorex* the long head is a strong muscle which originates from the axillary border of the scapula near the glenoid fossa and inserts into the groove on the proximal tip of the proximal crest of the olecranon. The long head does not originate in *Sorex* by two heads as Ärnbäck-Christie-Linde (1907) said is true of *Crocidura*.

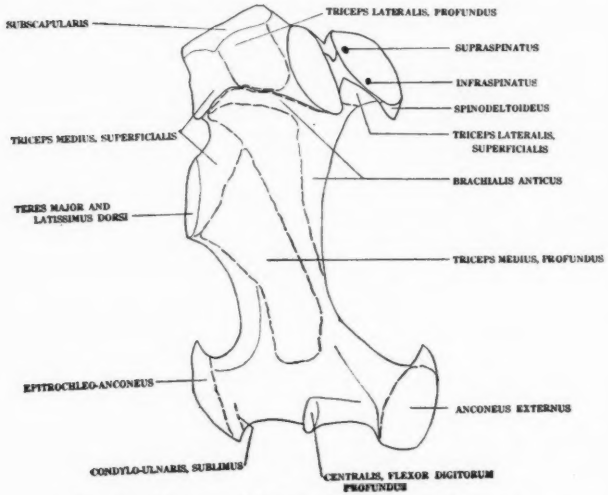

Fig. 31.—Humerus of *Neürotrichus gibbsii*, posterior view, showing areas of muscle attachments, ×10.

In *Sorex* the lateral head is a relatively large muscle which originates from the lateral side of the humerus, from the whole posterior side of the deltoid process, and from beneath the adjoining lateral overhang of the greater tuberosity. It inserts widely along the lateral side of the olecranon. The insertion is not fused with that of the other heads of the M. triceps, as Ärnbäck-Christie-Linde (1907) says is true of *Crocidura murina*.

The medial head in *Sorex* corresponds to the "anconaeus mediale" plus the "anconaeus quartus" of Ärnbäck-Christie-Linde (1907). The superficial medial head is a slim muscle which originates from the distal tip of the teres tubercle and from the medial surface of the shaft of the humerus immediately distally. It inserts on the medial side of the proximal crest of the olecranon. The insertion in *Sorex* is not fused with that of the other heads, as Ärnbäck-Christie-Linde (1907) stated is true for *Crocidura*. The deep medial head in *Sorex* originates from the distal third of the posterior surface of the shaft of the humerus and inserts beneath the long head upon the distal tip and anterior surface of the olecranon.

In *Neürotrichus* and *Scapanus* the medial and lateral heads of the M. triceps are both secondarily divided into deep and superficial parts, but all parts of the medial head are easily distinguished from all parts of the lateral head, since the main trunk of the radial nerve runs between them.

In *Neürotrichus* the long head originates from the anterior third of the axillary border of the scapula. The muscle fibers aggregate slightly to insert broadly upon the proximal crest of the olecranon.

The superficial part of the lateral head in *Neürotrichus* takes origin from the lateral edge of the greater tuberosity, beneath the deltoid process. The muscle runs distally and slightly posteriorly to insert upon the lateral edge of the proximal crest of the olecranon. The deep part of the lateral head is a long, slim muscle which originates from the posterior side of the lesser tuberosity of the humerus, runs distally, posteriorly, and slightly laterally, to insert upon the lateral edge of the proximal crest of the olecranon, covered by the insertion of the superficial lateral head.

The superficial part of the medial head of the M. triceps in *Neürotrichus* takes its origin from the posterior side of the teres tubercle and the posterior side of the medial portion of the lesser tuberosity. The muscle narrows distally and posteriorly to insert into the palmar aspect of the proximal crest of the olecranon. The deep part of the medial head is a thick, wide muscle lying beneath the superficial part. The origin is from the posterior shaft of the humerus distal to the origin of the superficial portion and continuing even into the olecranon fossa. The muscle inserts upon the palmar aspect of the proximal crest of the olecranon, deep to the insertion of the superficial part of the medial head.

In *Scapanus* the long head is similar to the same muscle in *Neürotrichus*, except that it is larger, thicker, and originates from the anterior two-thirds of the axillary border of the scapula. The insertion of this muscle and that of the superficial part of the medial head are partially fused.

The superficial part of the lateral head is short, thick, and has its origin from the superficial edge of the brachialis fossa beneath the greater tuberosity; its course and insertion are as in *Neürotrichus*. The deep part of the lateral head is almost continuous with the superficial part at the point of junction of the head of the humerus with the greater

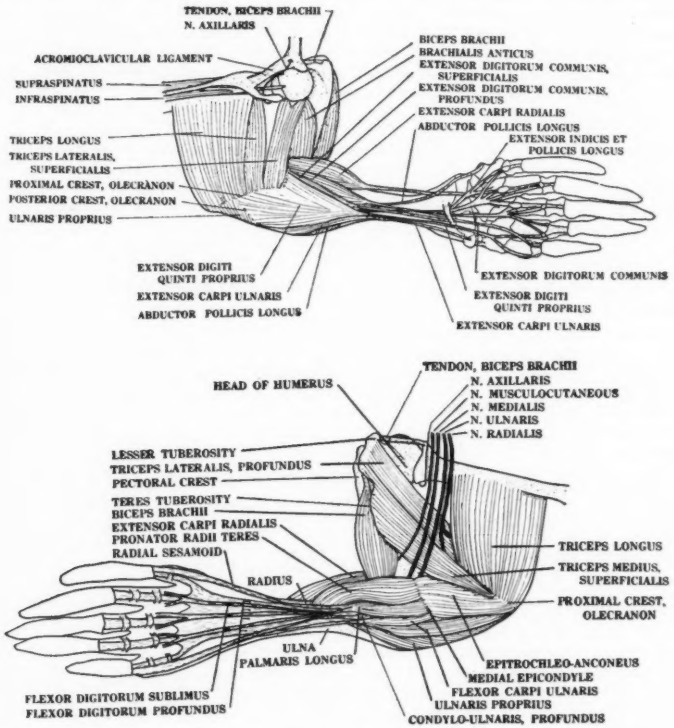

Fig. 32.—Deep muscles of the brachium and superficial muscles of the antebrachium of *Neürotrichus gibbsii*. A. Anconeal aspect, ×3.4. B. Palmar aspect, ×3.85.

tuberosity, and thus the two parts of the lateral triceps are not so widely separated as they are in *Neürotrichus*. Specifically, the origin of the deep part of the lateral head is from the posterior surface of the humerus immediately beneath the head of the humerus, from the medial side of the head, and from the groove between the head and the lesser tuberosity; its origin thus overlies the origin of part of the M. brachialis, as the origin of the superficial part overlies the remainder of the origin of the M. brachialis. Insertion is upon the anconeal surface of the proximal crest of the olecranon, deep to the insertion of the superficial part. The two parts of the lateral head can be told apart at their insertion by the difference in direction of their fibers.

In *Scapanus* the superficial part of the medial head is much larger than in *Neürotrichus*. It originates from the posterior side of the teres tubercle, from the adjacent shaft of the humerus, from the distal tip of the teres tubercle, from the anterior side of the distal portion of the teres tubercle (these latter fibers pass beneath the tubercle to join the remainder of the muscle), and from the surface of the M. latissimus dorsi as that muscle joins the M. teres major. From these extensive areas of origin the muscle aggregates and narrows to its insertion on the palmar half of the proximal process of the olecranon, deep to the insertion of the long head. The insertions of the superficial part of the medial head and that of the M. epitrochleo-anconeus are partly fused along their adjoining borders. The deep part of the medial head has its origin as in *Neürotrichus*. Insertion is into the cavity of the dorsal surface of the olecranon, as in *Sorex*. This is a thick, short, strong muscle, relatively larger than in *Neürotrichus* and with much greater areas of origin and insertion, due to the factor of greater bone surfaces available in *Scapanus*.

Innervation. All heads are innervated by branches of the N. radialis.

Action. The M. triceps is the great extensor of the forearm; due to their differences in position the various parts would operate more efficiently during different phases of the extensor movement. The long head, which has its origin more posteriorly than have the other parts of the muscle, would funtcion more efficiently when the antebrachium was flexed. Thus the long head would probably initiate the extensor movement. As extension continues, however, the long axis of the olecranon and the direction of pull of the long head of the M. triceps tend to become parallel, so that the muscle is functionless. Before this happens the more anterior parts of the muscle will contract and maintain the extensor action.

In the talpids extension of the antebrachium by the M. triceps does not directly contribute to the displacement of earth by the hand, since the plane of the palm of the hand is the same plane as that in which the antebrachium moves when extended or flexed. Thus extension or flexion of the forearm merely moves the hand through the earth sideways, an action which can have little effectiveness in digging. It is contraction of the great rotators of the humerus which pulls the flat of the manus through the earth in an effective digging stroke, but the action of the M. triceps controls the level at which that stroke occurs.

Discussion. The M. triceps probably reaches its greatest development in the talpine moles, which fact, correlated with the extreme length of olecranon and shortness of antebrachial shafts, would undoubtedly make it the most powerful triceps, relative to size of animal, among the tetrapods. The lateral head or the medial head, acting alone, would tend to rotate the antebrachium, but the nature of the elbow-joint precludes any possibility of such action except possibly in *Sorex;* however, such individual action by one or the other heads could brace the elbow-joint against forces acting in the opposite direction.

M. dorso-epitrochlearis (fig. 27).—Howell (1937b) believed that this small muscle arose by separation from the M. latissimus dorsi. In all soricoids investigated it originates from the superficial surface of the M. latissimus dorsi, immediately posterior to the insertion of that muscle, and runs over the medial side of the elbow to insert into the fasciae of the flexors of the forearm. The muscle is relatively broader in *Scapanus* than in *Sorex* or *Neürotrichus*.

Innervation. By a long, thin branch from near the base of the N. radialis.

Action. The muscle is obviously a tensor of the forearm fasciae, but the purpose of such action is unknown. It could not act as a flexor of the forearm, since it crosses the elbow-joint.

M. anconeus lateralis (figs. 30, 33).—This muscle is a derivative of the lateral head of the M. triceps (Howell, 1937b). In *Sorex* the M. anconeus lateralis is small; it originates from the tip of the lateral epicondyle of the humerus and runs over the elbow-joint to insert into the immediately adjacent lateral side of the ulna. The muscle would serve to pull the ulna against the humerus. The muscle is not mentioned by Ärnbäch-Christie-Linde in *Crocidura*, but she may have missed it due to its small size.

In *Neürotrichus* and *Scapanus* this is a short, wide muscle which originates broadly from the posterior surface of the external condyle of the humerus and fans out to insert deeply upon the anconeal edges of the proximal and posterior crests of the ulna.

Innervation. By a branch from the N. radialis.

Action. In *Neürotrichus* and *Scapanus* the muscle would assist the triceps in flexion of the forearm.

M. anconeus medialis.—This muscle is a derivative of the medial head of the triceps (Howell, 1937b), runs from the medial epicondyle to the olecranon, and is innervated by a branch from the radial nerve. If a muscle in this same location is innervated by a branch from the N. ulnaris, that muscle is assumed to be a derivative of the elbow matrix of the ventral division of the pectoral limb (Howell, 1936a, b) and is named the M. epitrochleo-anconeus. Since in *Sorex*, *Neürotrichus*, and *Scapanus* the muscle in this position was innervated in each instance by the N. ulnaris and not by the N. radialis, the M. epitrochleo-anconeus is present, but the M. anconeus medialis is not. Edwards (1937) described a twig of the N. radialis innervating his "anconeus internus" in *Scalopus*, but I could not find such innervation in any specimen dissected.

APPENDICULAR SYSTEM (PECTORAL LIMB)

VENTRAL (FLEXOR) DIVISION

INFRAZONAL GROUP

These muscles are mammalian representatives of variable muscular slips passing from the sternum and ribs to the coracoid bone in living reptiles (Howell, 1937b). This group of muscles is the most confusing encountered by me in the soricoid body. They have been given a wide variety of names but have never been adequately dissected or described. The innervation is of no help in determining their homologies, since they, as well as the anterior pectorals, are innervated by ventral branches of cervical nerves VI and VII. I have no certainty that my naming of these muscles is any more satisfactory than was that of my predecessors.

M. costoscapularis.—This is a muscle which Howell (1937b) described in therian mammals as having origin from the sternum and/or ribs, and inserting upon the scapula. Earlier (1936b) he had called the same muscle the "sternoscapualris." I did not find the muscle in any of the following shrews: *Sorex trowbridgii*, *Sorex palustris*, *Blarina brevicauda*, *Notiosorex crawfordi*, *Cryptotis* sp. Ärnbäck-Christie-Linde (1907) did not describe it in *Crocidura*. In the talpids, Freeman (1886) and Campbell (1939) homologized it with the soricid M. subclavius, while Edwards (1937) termed it a pectoralis minor. Dobson's (1883) interpretation was the same as is mine. In *Desmana* Dobson (1883: 151) described the muscle as being fused with the more dorsal M. subclavius; in *Condylura* Dobson apparently forgot to describe the muscle (or he missed it, which does not seem possible, as he described the M. subclavius, which lies deep to it). Campbell (1939) found the muscle in *Condylura* clearly divided into two parts; I shall consider these two parts in *Neürotrichus* and *Scapanus* as being separate muscles.

M. costoscapularis ventralis (figs. 27, 28).—In *Neürotrichus* this muscle is short, thick, and powerful; the origin lies immediately beneath the pectoral layer in common with the origin of the M. costoscapularis dorsalis from the posterior three-fourths of the keel of the manubrium, from the ventral surface and lateral edge of the wing of the manubrium, and

from the anterior edge of the cartilaginous part of the first rib. From the common origin the two muscles run anteriorly and laterally and divide; the ventral muscle is the larger and inserts upon the posterior surface of the distal two-thirds of the clavicle.

In *Scapanus* this short, thick muscle is not fused with any other; it originates from the greater part of the keel of the manubrium anterior to the level of the first rib and from the ventral and lateral surfaces of the wing of the manubrium. The fibers aggregate anteriorly and laterally to insert upon the tubercle and the distal half of the posterior side of the clavicle.

Innervation. N. subclavius.

Action. This muscle is a powerful retractor of, and brace for, the clavicle, and would keep the clavicle from being displaced anteriorly. In this way it braces the shoulder-joint and makes certain that the humerus will have a solid base (the clavicle) to thrust against in the digging stroke.

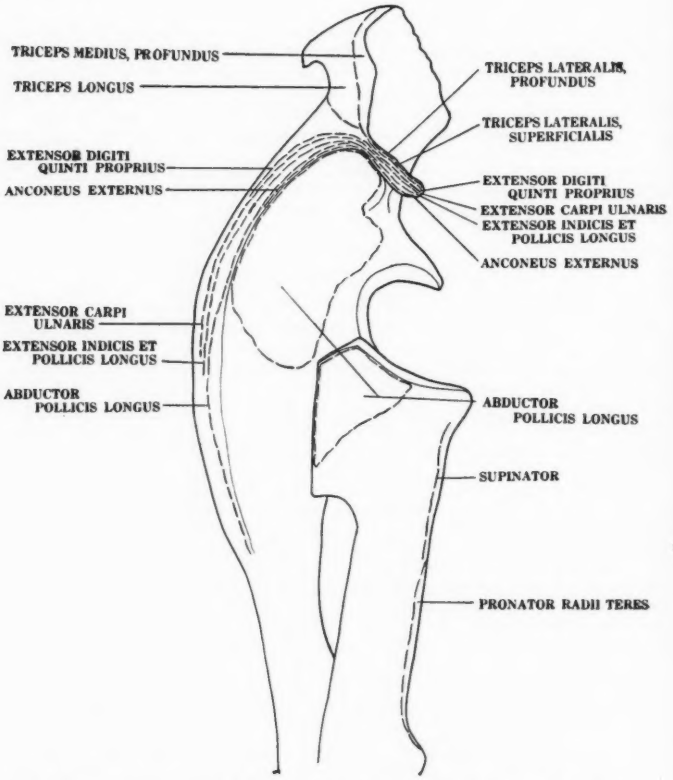

Fig. 33.—Proximal parts of the radius and ulna, anconeal view, *Neü.ot ichus gibbsii*, showing areas of muscle attachments, ×17.5.

Discussion. The M. subclavius, as described by Edwards (1937) in *Scalopus*, would seem to represent a part of my M. costoscapularis ventralis.

M. costoscapularis dorsalis (figs. 26, 28).—In *Neürotrichus* the origin is continuous with that of the ventral costoscapularis, as has been described. The two muscles separate and the dorsolateral and smaller portion runs anterolaterally across the dorsal surface of the clavicle to insert into the metacromion of the scapula.

In *Scapanus* this muscle is short but comparatively wide and strong; it originates from the dorsal side of the wing of the manubrium, runs transversely to the overlying M. subclavius, and has a wide insertion on the distal tip of the dorsal surface of the clavicle, upon the length of the acromioclavicular ligament, on the acromion of the scapula, and on the dorsal fascia of the M. supraspinatus immediately posterior to the acromion. The dorsal side of the muscle consists of a heavy, glistening fascia, which is continuous with the fascia of the M. supraspinatus and with the acromioclavicular ligament.

Innervation. From cervical nerves VI and VII by the N. subclavius.

Action. The muscle draws the anterior end of the scapula medially and slightly posteriorly and in *Scapanus* it tightens the acromioclavicular ligament and also assists the M. costoscapularis ventralis. In general, then, it serves to pull the shoulder-girdle medially and to brace it against the body, presumably at times of great activity of the humerus, such as in digging, when a firm support for the humerus is most needed.

Discussion. The M. costoscapularis, I presume, was present in the soricoid ancestor, but was lost in the soricid because, as a light semi-cursorial animal, it had no need for it. But the peculiar fossorial activities of the Talpidae demanded such a muscle to brace the shoulder-joint, so that it has beeen developed into a large muscle whose origin occupies most of the surface of the manubrium.

Freeman (1886) and Campbell (1939) did not dissect through this muscle to find the true M. subclavius dorsal to it, and so they gave the name "subclavius" to the M. costoscapularis.

Dobson's treatment (1883) of this muscle is confusing. In *Desmana* he described a M. sterno-clavicularis (my M. costoscapularis ventralis) and a M. sternoscapularus (my costoscapularis dorsalis), which muscles he says are fused with the M. subclavius, and the single muscle is then distributed to the clavicle and scapula. If this is true, *Neürotrichus* and *Desmana* have little in common in this region.

M. subclavius.—In *Sorex, Blarina, Notiosorex,* and *Cryptotis* this muscle lies immediately beneath the pectoralis complex. It originates from the anterior side of the cartilage of the first rib near the manubrium, runs laterally and slightly anteriorly to insert upon the dorsal side of the distal third of the clavicle. The muscle is the same in *Crocidura* (Ärnbäck-Christie-Linde, 1907). The action of the muscle in these shrews would be to brace the clavicle against the sternum and swing its distal end slightly posteriorly.

In *Neürotrichus* the muscle lies dorsal to the M. costoscapularis dorsalis; it is a small muscle which originates from the osseo-cartilaginous junction of the first rib. The muscle runs anteriorly and inserts upon the posterodorsal angle of the medial end of the clavicle.

In *Scapanus* the origin is from the lateral half of the anterior side of the first costal cartilage. The muscle runs directly anteriorly, parallel to, and at the same level as, the wing of the manubrium, to narrow and insert by a strong tendon into the medial edge of the posterior side of the clavicle, near the dorsal border. The ventral side of the muscle is covered with glistening fascia where the M. costoscapularis dorsalis crosses it transversely.

Innervation. From cervical nerves VI and VII, by the N. subclavius.

Action. In *Neürotrichus* and *Scapanus* the muscle could act as a brace to the clavicle, to keep it from being displaced forward, or it could pull the first rib anteriorly.

Discussion. As has been mentioned, Freeman (1886), Campbell (1939), and Edwards (1937) did not dissect deeply enough to find this muscle. Only Dobson (1883: 151, 167) mentioned it in *Desmana* and *Condylura*, but in *Desmana* he stated that it is fused with the Mm. costoscapulari. I suspect that actually Dobson did not dissect deeply enough in *Desmana* to find the muscle, and so assumed that it had fused with those he did find.

As previously mentioned, the muscle described by Edwards (1937) as the M. subclavius in *Scalopus* must be considered as a part of the M. costoscapularis ventralis.

VENTRAL (FLEXOR) DIVISION, SHOULDER GROUP, PECTORAL COMPLEX

This group represents the original pectoral musculature of the reptile lying between the sternum and the humerus (Howell, 1937b).

M. cutaneous maximus.—This dermal muscle is included here because of its insertion upon the humerus and because it is a derivative of the pectoral musculature. Howell (1937b) stated that the typical insertion is upon the humerus distal to the greater tuberosity; certainly he meant the lesser tuberosiy, since in every mammal known to me the muscle at the humerus is closely associated with the posterolateral pectoral musculature and with the M. latissimus dorsi. As the muscle is found in the soricoids, it inserts into the pectoral process and/or the groove between the lesser tuberosity and the pectoral process; Campbell (1939) described it in some detail in a larger series than I dissected. Primarily it is a muscle for movement of the skin, but theoretically it could aid in retraction and rotation of the humerus if the dermal ends were fixed; that the muscle ever accomplishes this action would have to be determined by physiological experiments upon living animals.

The innervation in *Scapanus* is from the cervical nerve VIII and thoracic nerve I. Innervation was not determined in the other two genera.

M. pectoralis profundus.—The M. pectoralis minor represents, according to Howell (1937b) the greater part of the original pectoral muscle of the reptile between sternum and humerus; in mammals it lies deep to the M. pectoralis major, which was originally a procoracoid-humeral muscle. As Howell says, however, there is no way to distinguish minor from major elements once the procoracoid has disappeared, except that the superficial sheet is usually th major. Thus the muscle designated as the M. pectoralis profundus by Campbell (1939) and myself is probably the true pectoralis minor.

In *Sorex* this muscle originates from the ventral midline of the sternum between the third and seventh ribs. It is a thicker muscle than the M. pectoralis superficialis posticus and narrows but little to its insertion deep to the posterior part of that muscle upon the full length of the pectoral process. In *Crocidura* (Ärnbäck-Christie-Linde, 1907) and *Blarina* (Campbell, 1939) the origin is more extensive, from the second rib to the xiphoid process. In these shrews the posterior part of the muscle may be derived from the superficialis (major?) layer, which does not extend posteriorly as far as one might expect.

Dobson (1883) did not describe this muscle for *Desmana;* Campbell (1939) stated that it is absent in *Galemys,* but that he found it "in the rest of the Talpidae." Be that as it may, I could not find the muscle in *Neürotrichus;* if present it is fused with the M. pectoralis superficialis posticus and does not have a separate twig of innervation.

In *Scapanus* the origin is from the dorsal portion of the manubrium between the first and second ribs and from the median ends of the costal cartilages of the first two ribs. The muscle runs anterolaterally and inserts on the lateral half of the pectoral ridge; it is the only pectoral muscle to insert there.

Innervation. From cervical nerves VII and VIII and thoracic nerve I.

Action. In *Sorex,* whether the humerus is in an extended or retracted position, the muscle would adduct it ventrally upon the thorax. In *Scapanus* the action is different; movement of the pectoral crest toward the bases of the first and second ribs causes a depression of the distal end of the humerus, which controls the height at which the digging action occurs. The action in the mole is true adduction, inasmuch as the humerus is depressed and its medial edge brought towards the thorax; such adduction in the shrew, where the primitive condition of the arm is retained, is attained by the muscle acting as the power in a lever of the third class, whereas in *Scapanus* the pectoral crest (the point of power application) is proximal to the greater tuberosity and the head of the humerus (both of which act as fulcra), so that the system is a lever of the first class.

M. pectoralis abdominalis.—This derivative of the deep pectoral group is absent in *Sorex.* In *Neürotrichus* and *Scapanus* it is a thin, narrow bundle of muscular fibers which arises from the fascia of the Mm. rectus abdominalis and obliqus externus, lateral to the main mass of the M. pectoralis superficialis posticus; it runs parallel to the latter muscle, and is inserted with the most lateral part of it.

Innervation. Not determined.

Action. Assists the more posterior fibers of the M. pectoralis superficialis posticus; strengthens the abdominal wall.

SHOULDER GROUP, ANTERIOR CORACOID (PROCORACOID) COMPLEX

These are the muscles which Howell (1937b) has found ran from the procoracoid to the humerus in primitive tetrapods, but which, with the disappearance of the procoracoid, shifted their origins.

M. pectoralis superficialis.—As this is the most superficial pectoral muscle it is probably the true pectoralis major, but since the posterior part of the major may have been given up to the M. pectoralis profundus in the Soricidae, and since the minor may have fused with the major in *Neürotrichus, Galemys,* and *Desmana,* it was thought best to evade the issue of strict homology by giving the muscle in question the name of "superficialis."

In all genera dissected the muscle is separated functionally into two parts; one part lies anterior to the shoulder-joint and the second lies posterior to it. The two parts are contiguous but are separated by a fascial plane; along this fascial plane the muscle fibers lie parallel, but diverge anterior and posterior to it. For this reason the muscle has been divided for convenience into a pars anticus and a pars posticus.

M. pectoralis superficialis anticus (figs. 27, 31).—In all soricoids observed, the origin of the pars anticus lies partly anterior to the manubrium; this anterior part takes origin from a midline raphe which is shared by the same muscle of the other side. The part of the muscle originating from the raphe is much thicker than the part originating from the manubrium.

In *Sorex* the muscle takes origin from the midline raphe and from the ventral midline of the anterior half of the sternum. The fibers converge laterally to insert on the crest of the distal half of the pectoral ridge.

In *Neürotrichus* the muscle originates from the ventral surface of the anterior third of the manubrium and from the median raphe, which extends 0.5 cm. anterior to the manubrium. The fibers do not converge, but run laterally over the ventral surface of the cleidohumeral joint to insert upon the length of the pectoral process of the humerus.

In *Scapanus* the muscle originates mostly from the midventral raphe and only in small part from the anterior end of the sternum. The muscle runs laterally, superficial to the Mm. cleidodeltoideus and acromiodeltoideus, to insert as in *Neürotrichus.*

Innervation. From cervical nerves VI and VII, by a ventral (anterior) thoracic which also serves the anterior end of the M. pectoralis superficialis posticus, so that the anticus and posticus portions of this muscle are seen not to be fundamental entities, but merely functional divisions of a single muscle.

Action. In *Sorex* the muscle would adduct the humerus toward the thorax; I do not believe, however, that the shrew is capable of extending the humerus forward and then adducting it upon the cervical region. In *Neürotrichus* and *Scapanus* the muscle aids in recovery after the digging stroke. At the end of the digging stroke the humerus has been retracted and the true medial border rotated posteriorly; contraction of the M. pectoralis superficialis anticus will then pull the humerus anteriorly and assist in rotating it back to its normal position with the true medial border facing ventrally or ventrolaterally.

M. pectoralis superficialis posticus (figs. 27, 28, 30).—In *Sorex* this is a thin muscle which originates along the ventral midline of the sternum between the center of the manubrium and the fourth rib; similar restricted areas of origin have been noted for *Crocidura*

(Ärnbäck-Christie-Linde, 1907) and *Blarina* (Campbell, 1939); the possibility that the posterior part of the muscle has fused with the M. pectoralis profundus has been mentioned previously.

In *Neürotrichus* the M. pectoralis superficialis posticus is large, powerful, and originates from the entire lateral and ventral surfaces of the sternum, from the anteroventral surface of the xiphisternum, from the median portions of the second to seventh costal cartilages, and from the ventral portion of the lateral side of that part of the manubrium lying posterior to the clavicles. The fibers aggregate to insert across the lesser tuberosity, across the bicipital tunnel, and into the posterior surface of the pectoral crest.

In *Scapanus* the muscle is extremely thick and powerful; it originates exactly as in *Neürotrichus,* but has a relatively greater extent of origin due to the greater length of manubrium. The fibers aggregate anteriorly and laterally to insert upon the true medial half of the petcoral crest (which lies, of course, lateral to the insertion of the M. pectoralis profundus, which inserts on the true lateral half of the same crest; it must be remembered at all times that the humerus extends dorsally).

Innervation. The anterior part of the muscle is served by twigs of the same ventral thoracic nerve which innervates the pars anticus; the posterior part of the muscle is innervated from cervical nerves VII and VIII and thoracic nerve I by a ventral thoracic nerve which also serves the M. pectoralis profundus.

Action. In *Sorex* the muscle attempts to adduct the humerus posteriorly upon the thorax. In *Scapanus* the more anterior fibers would have the same action as does the M. pectoralis profundus, but the more posterior fibers, whose attachments on the humerus are more distal from the midline and whose pull is more posterior in direction, would assist the Mm. teres major, subscapularis, and latissimus dorsi in retraction and rotation of the humerus. In *Neürotrichus,* which has no M. pectoralis profundus, the anterior fibers of the pars posticus would depress the humerus; the posterior fibers would retract and rotate the humerus, and those between would partake of both functions.

Discussion. This is one of the largest and most powerful muscles in the body of *Scapanus,* and is only relatively less so in *Neürotrichus* because it is shorter. This hypertrophy is to be explained on the basis of the muscle acting in conjunction with the other strong retractors and rotators of the humerus in the digging stroke.

M. supraspinatus (figs. 29, 31, 32).—In *Sorex* this is a thick, strong muscle which originates from the whole anterior side and crest of the scapular spine and from the whole of the supraspinous fossa. The fibers converge ventrally to a strong tendon which runs beneath the acromion and inserts across the shoulder-joint into the postero-proximal angle of the greater tuberosity.

In *Neürotrichus* the origin is from the supraspinous fossa, from the supraspinous surface of the scapular spine, and from the intermuscular septum which this muscle shares with the M. subscapularis. The muscle runs beneath the acromioclavicular ligament, and inserts across the scapulohumeral joint into the cleidohumeral joint at the medioproximal angle of the posterior side of the greater tuberosity.

In *Scapanus* the origin, position, and insertion are as in *Neürotrichus.*

Innervation. From cervical nerve VI by the N. suprascapularis.

Action. In the three genera dissected, and presumably in all soricoids, the muscle extends the humerus and acts as a counterrotator to the action of the Mm. teres major, subscapularis, pectoralis superficialis posticus, and latissimus dorsi.

M. infraspinatus (figs. 26, 29, 31, 32).—In *Sorex, Neürotrichus,* and *Scapanus* this muscle originates from the whole of the infraspinous fossa, but not from any part of the scapular spine. In *Sorex* the muscle runs beneath the metacromion and inserts on a narrow area on the proximal edge of the deltoid process and the distal portion of the greater tuberosity. In *Neürotrichus* and *Scapanus* the fibers aggregate to a small, strong tendon which crosses the scapulohumeral joint and inserts upon the posterior surface of the greater tuberosity, distal to the insertion of the M. supraspinatus but proximal to the deltoid process.

Innervation. N. suprascapularis. In all specimens of *Scapanus* dissected, the nerve,

after passing through the M. supraspinatus, penetrated a foramen in the acromion to reach the M. infraspinatus. In some skeletons which I have observed, however, no such foramen is present in the scapulae; in these specimens the nerve undoubtedly proceeded around the anterior end of the acromion to reach the M. infraspinatus.

Action. The muscle would assist the Mm. supraspinatus and spinodeltoideus as a counter-rotator to the great digging muscles. In *Sorex* the muscle can assist in flexion of the humerus, but in *Neürotrichus* and *Scapanus,* where there has occurred a distal and posterior migration of the greater tuberosity and the head of the humerus, the tendon attaches at the level of these fulcra and could have no function as a flexor.

Discussion. The M. infraspinatus is small in all of the soricoids, and relatively smaller in the more fossorial forms; its complete absence in *Talpa* and *Mogera* has been mentioned (p. 537). The small size and eventual disappearance of this muscle in the talpids can be correlated in part with the approximation of scapular spine and axillary border and the final fusion of these parts of the scapula, so that the infraspinous fossa is obliterated. But even so, if the muscle were useful it could be retained by a shift of origin or by being contained within an infraspinous tunnel; the anterior part of it, at least, might be retained. With this idea in mind I examined a specimen of *Mogera hainana,* but could find no remnant of the M. infraspinatus, unless it has fused completely with the M. spinodeltoideus. The N. suprascapularis would have to be traced carefully to settle such a point, but the specimen of *Mogera* available was not well enough preserved for this.

Freeman (1886), dissecting *Talpa* alone, did not realize that the M. infraspinatus was absent and assigned that name to the M. spinodeltoideus. Dobson (1883) separated the infraspinatus from the overlying deltoid (M. spinodeltoideus) in *Desmana,* but failed to distinguish them in *Condylura.*

It is difficult to account for a lack of use for the M. infraspinatus; among therian mammals the muscle is lost only in *Talpa* and *Mogera* (Howell, 1937b). Certain counter-rotators to the action of the great digging muscles are needed, although one other muscle of this functional group, the supraspinatus, is also small in size (table 34). Campbell (1939) suggested that perhaps the M. pectoralis superficialis anticus has become the chief counter-rotator of the humerus; certainly it is an important one. In addition the M. biceps brachii acts as a counter-rotator of the humerus in most talpids (p. 642). If the Mm. pectoralis superficialis anticus and biceps brachii have taken over the major counter-rotator roles in the talpids, the hypertrophy of the M. spinodeltoideus must be explained chiefly on the basis of its action as a flexor, but I believe that it retains strong counter-rotator possibilities. In any case, the reduction and eventual loss of the M. infraspinatus is not satisfactorily understood, unless it be due to its loss of flexor action in the fossorial and semi-fossorial talpids.

SHOULDER GROUP, CORACOID (POSTERIOR CORACOID) COMPLEX

The Mm. coracobrachialis represents those muscles whose origins in the lower tetrapods lay upon the true coracoid, but in mammals originate from the coracoid process (Howell, 1937b). None of these muscles have ever been reported for any talpid; I found none in *Sorex, Neürotrichus,* or *Scapanus;* Arnbäck-Christie-Linde (1907) did not mention them for *Crocidura,* nor Campbell (1939) for *Blarina.* (The M. biceps brachii is not a member of this complex, since it was primitively a muscle of the elbow.)

VENTRAL (FLEXOR) DIVISION, ELBOW (BRACHIO-ANTEBRACHIAL) GROUP, BRACHIAL COMPLEX

These are flexor muscles which originally bridged the elbow, but whose origins have migrated proximally, so that they have become more efficient as antebrachial flexors (Howell, 1937b).

M. brachialis (figs. 30-32, 34).—In *Sorex* the origin of this muscle lies under all others on the posterior side of the humerus, from the lesser tuberosity completely around the humerus, below the head, to the greater tuberosity. The muscle spirals around the

lateral side of the humerus to a flat tendon on the anterior surface; this tendon lies adjacent to, but lateral from, the tendon of the M. biceps brachii. Most of the tendon fuses with the tendon of the M. biceps brachii, and inserts as described for that muscle; the remainder inserts upon the anterior surface of the shaft of the radius, immediately distal to the head of the radius.

In *Neürotrichus* the muscle has a wide area of origin from the posterior surface of the humerus, immediately distal to the greater tuberosity, lesser tuberosity, and head of the humerus, from the lateral surface of the humerus between the greater tuberosity and the end of the pectoral ridge, and from the distal tip of the pectoral ridge. The fibers course around the distal part of the lateral side of the humerus, and the muscle inserts by a flat tendon into the palmar surface of the ulna, close to the elbow-joint. Those fibers from the distal tip of the pectoral ridge run muscularly, without joining the tendon, and form the most proximal part of the insertion. The tendon of this muscle lies between the elbow-joint and the tendon of the M. biceps brachii.

In *Scapanus* the origin is as in *Neürotrichus* except that it also originates from the greater part of the brachialis fossa, from the posterior and lateral surfaces of the shaft of the humerus deep to the origin of the lateral head of the M. triceps, and from the lateral supracondyloid ridge deep to the origin of the M. extensor carpi radialis. The muscle passes around the lateral side of the humerus between the distal end of the pectoral ridge and the lateral epicondyle and passes deep to the M. biceps brachii to insert upon the ulna as in *Neürotrichus*, but muscularly. It is relatively a more powerful muscle than in *Neürotrichus*.

Innervation. N. musculocutaneus.

Action. Flexor of the antebrachium, with the M. biceps brachii.

Discussion. Campbell (1939) believed that the M. brachialis replaces the M. triceps as the chief antigravity muscle acting over the elbow-joint, and that the mole, like the sloth, is an animal which relies upon at least one brachial flexor muscle for posture. This statement requires some study and is not, in my opinion, wholly correct. In attempting locomotion on a plane surface a true mole is faced with the problem that its humerus projects dorsally; to touch the floor with the hand it is obvious that the forearm must be flexed, and if it is to such a situation that Campbell is referring, he is correct in stating that the M. brachialis replaces the M. triceps as the chief antigravity muscle acting across the elbow. But a talpine's normal progression is through a cylinder with soft sides, into which it can dig its claws. In other words, the forearm can project laterally at a right angle from the humerus, and under these more normal conditions the Mm. brachialis and triceps would act synergistically to maintain the elbow-joint at a right angle; rotation backward of the outside edge (medial border) of the humerus would then draw the forearm and manus posteriorly, and anterior locomotion would result. Under these circumstances the Mm. brachialis and triceps act equally as antigravity muscles to maintain the posture of the body while in locomotion.

M. biceps brachii (figs. 27, 29, 32, 34).—In all soricoids investigated there has been found but one head of origin to this muscle; presumably this head is homologous to the long head of those mammals whose M. biceps brachii has two heads.

In *Sorex* the muscle originates from the coracoid border of the rim of the glenoid fossa, runs through the shoulder-joint, through the bicipital (intertubercular) groove, and expands into a fleshy belly on the anterior side of the humerus. Distally the tendon of insertion fuses with most of the tendon of insertion of the M. brachialis; the united tendon then splits to insert into the medial sides of the ulna and the radius immediately distal to the elbow-joint. A comparable insertion exists in *Blarina* (Campbell, 1939). In *Crocidura* (Arnbäck-Christie-Linde, 1907) the two muscles fuse fleshily and insert as in *Sorex*.

The tendon of origin of the M. biceps brachii traverses a bicipital tunnel which crosses the proximal end of the humerus at right angles in all genera of the Talpidae except *Uropsis*, *Galemys* (Campbell, 1939, figs. 33-34) and presumably *Desmana*. In *Neürotrichus* and *Scapanus* origin is from the same point on the scapula as in *Sorex*; the tendon crosses the shoulder-joint on the medial side of the head of the humerus and turns at

nearly a right angle to enter the bicipital tunnel. In *Neürotrichus* the tendon emerges from the bicipital tunnel on the anterior face of the humerus, but in *Scapanus*, in other talpines, and in *Condylura* the bicipital tunnel emerges on the posterior side of the humerus. due to the extreme transverse growth of the pectoral crest, and the tendon must pass through the bicipital groove to regain its normal position on the anterior surface of the humerus. In all talpids the large muscular belly occupies most of the anterior surface of the humerus. In *Neürotrichus* the single tendon of insertion runs between the Mm. extensor carpi radialis and the pronator radii teres and then between two hads of the M. flexor digitorum profundus (heads radialis proprius and condylo-radialis) to insert upon the dorsal edge of the radius, distal to the elbow-joint. In *Scapanus* the muscle splits into two parts, which insert fleshily upon the anconeal-pollical and palmar-pollical surfaces of the

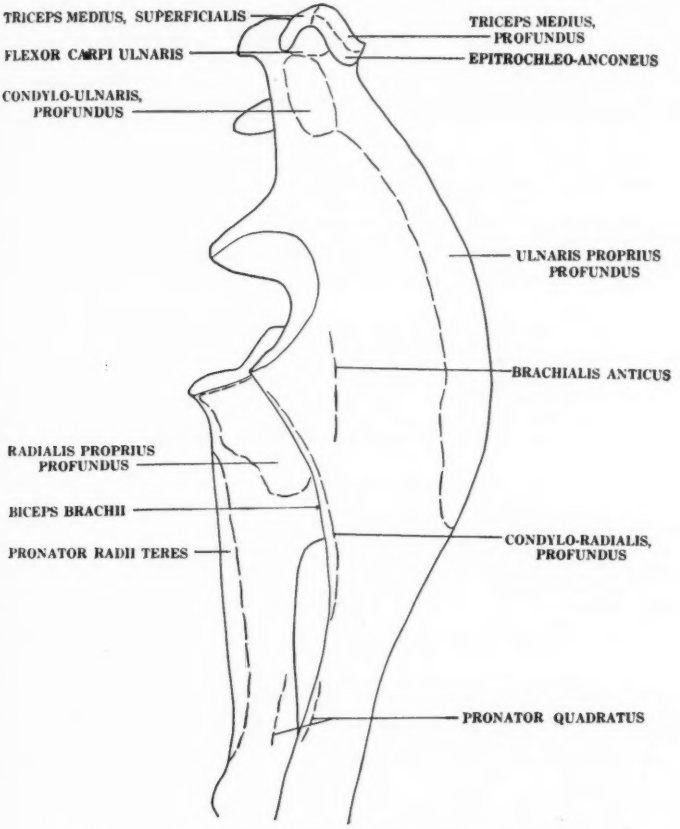

Fig. 34.—Proximal parts of the radius and ulna, palmar view, *Neürotrichus gibbsii*, showing areas of muscle attachments, ×19.

radius, deep to the insertion of the M. pronator radii teres. In *Scapanus* this insertion upon the radius is midway of the length of that bone, and some of the surface fascia of the M. biceps brachii is continuous with the fascia of the dorsum of the manus. The M. pronator radii teres originates so proximally upon the humerus and the M. biceps brachii emerges upon the anterior surface of the humerus so far distally that the two muscles are contiguous and practically parallel. In contrast, the M. brachialis in *Scapanus* inserts so proximally that its fibers lie at right angles to those of the M. biceps brachii.

Innervation. N. musculocutaneus.

Action. Flexor of the forearm. In addition, in those talpids in which the tendon of origin of the M. biceps brachii crosses the proximal end of the humerus transversely in the bicipital tunnel, the muscle is a counter-rotator of the humerus, inasmuch as contraction of the muscle will tend to straighten the tendon so that it can all lie in one longitudinal plane; such action will draw the true medial border of the humerus anteriorly and assist the identical action of the Mm. supraspinatus, infraspinatus, and pectoralis superficialis anticus. The M. biceps brachii, in these talpids, thus serves a double function in the recovery after a digging stroke; the muscle flexes the forearm and rotates the humerus anteriorly. Freeman (1886), describing the shoulder of *Talpa*, was the first to discuss this unique capability of this muscle.

Discussion. The fact that neither supraglenoid tubercle nor coracoid process can be distinguished on the scapula of a soricoid has led to some question as to the homology of the single head of the M. biceps brachii in this group. The fact that in a generalized soricoid, as *Sorex*, the tendon of origin always penetrates the capsule of the shoulder-joint and runs in a bicipital groove has led most investigators to assume that the single head was the homologue of the long head of other mammals; Howell (1937b) has said that such an assumption is not necessarily true, as in mammals the two heads may fuse and origins of this fused head or of either single head may shift their locations.

APPENDICULAR SYSTEM (PECTORAL LIMB), DORSAL (EXTENSOR) DIVISION, ELBOW MATRIX, ANTEBRACHIAL GROUP

These are extensor muscles which spanned the elbow in primitive tetrapods, but whose insertions, for the most part, have moved distally onto the manus. This group of muscles was divided by Howell (1936a) and Straus (1941) into three basic groups: Extensor humero-radialis (medial), extensor humero-dorsalis (intermediate), and extensor humero-ulnaris (lateral).

EXTENSOR HUMERO-RADIALIS DIVISION

M. brachio-radialis.—This muscle is absent in all insectivores (Straus, 1941). I found no indication of it in the three genera dissected.

M. supinator (figs. 30, 33).—Straus (1941) assigned the M. supinator to this group, although Howell (1936a) believed that it was originally a wrist muscle which has migrated to the elbow; he admitted, however, the possibility that it could belong in the humero-radialis group.

Among the soricoids this muscle has been previously described only in shrews (Ärnbäck-Christie-Linde, 1907), but I found it in both of the talpid genera I dissected. In *Sorex* it is a short, narrow, weak muscle which originates from the anterior edge of the lateral condyle of the humerus, covered by the origins of the Mm. extensor carpi ulnaris and extensor digitorum communis. The muscle runs medially and distally to insert onto the anterior surface of the proximal fifth of the radius.

In *Neürotrichus* and *Scapanus* the origin lies deep upon the anterior side of the lateral epicondyle of the humerus and the insertion is upon the proximal sixth of the pollical-anconeal surface of the radius. The muscle consists of only a few fibers in *Neürotrichus*, but is relatively stronger in *Scapanus*.

Innervation. N. radialis.

Action. Supination in the soricoid forearm would seem to be impossible, due to the

nature of the joints at elbow and wrise (p. 561). The muscle can, therefore, act to strengthen the elbow; it can act as a weak flexor of the forearm, or both. The extremely small size would indicate that it could have little function, but its retention in *Scapanus* would indicate some degree of importance.

Discussion. The deep branch of the radial nerve to the forearm passes beneath this muscle in each genus. Arnbäck-Christie-Linde (1907) stated that in *Crossopus* and *Sorex* the insertions of the Mm. supinator and pronator radii teres are fused; this is not true for *Sorex trowbridgii*. Dobson (1883: 153) stated that the muscle is absent in *Desmana* and he did not mention it for *Condylura;* Edwards (1937) did not mention is in *Scalopus*. I suspect that they missed it due to its small size.

M. extensor carpi radialis (figs. 30, 32).—In *Sorex* this is, for the forearm, a comparatively large, fusiform muscle, of which the distal two-thirds are tendinous; it is the deepest upon the forearm of the extensor group, a condition explained by Straus (1941) as due to its migration beneath the other forearm muscles. The muscle and its tendon run the length of the anterior side of the radius, through the shallow groove in the anterior surface of the distal end of the radius, beneath a transverse ligament of its own, and, at that level, divides into two tendons, of which the medial is the weaker. The lateral tendon inserts on the dorsal surface of the proximal end of metacarpal III, the medial inserts in the connective tissue between metacarpals II and III.

In *Neürotrichus* the origin is as in *Sorex*, except that a small part of the origin is also from the most proximal tip of the lateral epicondyle of the humerus and the insertion is broadly continuous on the dorsal surfaces of metacarpals II and III.

In *Scapanus* the muscle has the same position and relationships as in *Sorex* and *Neürotrichus*, but the area of origin is larger, consisting of the whole deeper surface of the spine of the lateral epicondyle and the whole of the lateral supracondyloid ridge. The insertion is as in *Neürotrichus*.

Innervation. N. radialis.

Action. General extensor of the manus at the wrist.

Discussion. This single muscle probably represents a fusion of the Mm. extensor carpi radialis longus and extensor carpi radialis brevis, the insertions of which in most mammals are upon metacarpals II and III, respectively.

ANTEBRACHIAL GROUP, EXTENSOR HUMERO-DORSALIS DIVISION

M. extensor digitorum communis (figs. 30, 32).—This muscle, the only one present in the humero-dorsalis division, was originally an extensor of the hand at the wrist, but has extended its insertions distally until in mammals it is primarily concerned with phalangeal extension (Straus, 1941).

In *Sorex* this is a fusiform muscle which appears to be rather small for the number of tendons it has. It originates from the lateral epicondyle of the humerus superficial to the origin of the M. extensor digiti quinti proprius. The muscle becomes tendinous midway of the antebrachium and immediately splits into three tendons, which run beneath the dorsal transverse ligament of the wrist and spread out upon the dorsal surface of the manus.

The insertion in *Sorex* is complex. The most medial tendon splits into two parts at the level of the transverse ligament; these two have a cross connection; and then the more medial inserts upon the distal phalanx of digit II; the more lateral inserts upon the distal phalanx of digit III. The central tendon of the three main ones, after receiving a cross connection from the lateral tendon midway of metatarsal IV, inserts into the distal phalanx of digit IV. The lateral of the three main tendons has an exceedingly complex insertion. At the level of the proximal end of metatarsal V it gives off a median slip which fuses with the tendon of the M. extensor indicis et pollicis longus to digit III. Immediately distally there is given off another slip medially; this fuses with the middle tendon from the M. extensor digitorum communis. At the same level another slip leaves, also medially, to

insert upon the dorsolateral angle of the distal end of metatarsal III. The main tendon then continues, to insert upon the dorsal surface of phalanx 2 of digit V.

In *Neürotrichus* the muscle arises by two heads, superficial and deep. The superficial head is a flat, narrow, fusiform muscle, which arises from the anterior surface of the lateral epicondyle of the humerus, deep to the origin of the M. extensor carpi ulnaris. The small tendon runs beneath the dorsal transverse ligament, continues out the medial side of digit V, and inserts upon the mediodorsal surface of the distal phalanx of digit V. The deep head takes origin from the anterior surface of the lateral epicondyle of the humerus, beneath the origin of the superficial head. It immediately divides into two parts, the tendons of which run through the dorsal transverse ligament. These two tendons then diverge and, after some intricate dividing and reuniting (fig. 32), the lateral tendon inserts on the distal phalanges of digits III and IV, the medial one upon the distal phalanges of digits I, II, and III.

The muscle in *Scapanus* is completely divided into three heads, all of which take origin from the proximal part of the lateral epicondyle, deep to the origin of the M. extensor digiti quinti proprius. The tendons of all run beneath the dorsal transverse ligament. The smallest and most superficial head divides at the distal end of the muscle into two tendons, which insert on the medial side of the distal phalanges of digits IV and V. A second head, deep to the first, has a tendon which divides at the level of the proximal ends of the metacarpals into two tendons; of these the weaker inserts on digit IV with the tendon from the first head, and the stronger inserts upon the dorsal surface of the distal phalanx of digit III. A third head, almost as large as the second, originates immediately beneath it; actually the second and third heads are not completely separable at their origins, so that the condition of the heads is essentially similar to that in *Neürotrichus*. The single tendon of this third head inserts on the dorsal surface of the distal phalanx of digit II.

Innervation. Deep radial nerve.

Action. The muscle is a phalangeal extensor of all digits in *Neürotrichus*, and of digits II to V in *Sorex* and *Scapanus*.

Discussion. In *Crocidura* (Ärnbäck-Christie-Linde, 1907) and *Desmana* (Dobson, 1883: 153) this muscle and the M. extensor digiti quinti proprius are fused at their origins; not only is this not true in the genera dissected by me, but the tendency is the opposite, since the M. extensor digitorum communis breaks up into separate heads. In *Sorex* the muscle was not divisible into separate heads, although the tendons were immediately divided. Straus (1941) stated that a pollical slip of this muscle is a specialized mammalian feature. I know of no adaptational factor to account for this extra slip in *Neürotrichus*.

ANTEBRACHIAL GROUP, EXTENSOR HUMERO-ULNARIS DIVISION

M. extensor digiti quinti proprius (figs. 30, 32, 33).—In *Sorex* this is a small fusiform muscle which lies superficially on the lateral side of the antebrachium between the Mm. extensor carpi ulnaris and the extensor digitorum communis. It originates from the lateral epicondyle of the humerus, immediately proximal to the origin of the M. extensor carpi ulnaris. The tendon of the muscle runs between the tendons of the Mm. extensor carpi ulnaris and the extensor digitorum communis, under the transverse ligament of the wrist, and then upon the dorsal surface of metacarpal V. Here it divides into two, which insert upon the distal phalanges of digits IV and V; the tendon to digit IV runs under the tendon of the M. extensor digitorum communis to digit V.

In *Neürotrichus* this is the most superficial muscle on the lateral surface of the forearm and consists of two wide, flat, fusiform heads, which lie side by side and are connected by a sheet of fascia. One of these heads originates superficially from the crest of the lateral epicondyle of the humerus, the other from the dorsal half of the proximal crest of the olecranon and from the posterior crest of the ulna. The two heads fuse into a single tendon which runs distally, outside of and lateral to the transverse ligament of the wrist and, at the level of metacarpal V, divides into two tendons, which insert as in *Sorex*.

In *Scapanus* the origin of this muscle is similar to that in *Neürotrichus*, but it is a

TABLE 37.—Muscles of the forearm

Ärnbäck-Christie-Linde, *Crocidura*	Dobson, *Desmana*	Dobson, *Condylura*	Edwards, *Scalopus*	Reed, Soricoidea
1. Epitrochleo-anconeus	Anconeus epitrochlearis vel internus	Anconeus internus	Anconeus internus	Epitrochleo-anconeus
2. Palmaris longus	Palmaris longus	Palmaris longus	Palmaris longus	Palmaris longus
3. Fl. brevis digitorum manus	(Not mentioned)	(Not mentioned)	(Not mentioned)	"Not found"
4. Fl. carpi ulnaris	Fl. carpi ulnaris	(Not mentioned)	Fl. carpi ulnaris	Fl. carpi ulnaris
5. Pronator radii teres	Pronator radii teres	Pronator radii teres	Pronator teres	Pronator radii teres
6. Flexor digitorum sublimus	Flexores digitorum sublimes et profundi	Fl. digitorus sublimus	(Overlooked)	Fl. digitorum sublimus
7. Fl. digitorum profundus		Fl. digitorum profundus	Fl. digit profundus, and Fl. digit. sublimus	Fl. digitorum profundus
8. Fl. carpi radialis	Fl. carpi radialis	(Not mentioned)	(Not mentioned)	Fl. carpi radialis
9. Supinator brevis	"Absent"	"Absent"	(Not mentioned)	Supinator
10. Ext. digitorum communis et digiti minimi	Ext. communis digitorum et minimi digiti	Ext. communis digitorum	Ext. (Minimi) digiti proprius, and Ext. digitorum communis	Ext. digitorum communis
11.		Ext. minimi digiti		Ext. digiti quinti proprius
12. Ext. carpi ulnaris	Ext. carpi ulnaris	Ext. carpi ulnaris (?)	Ext. carpi ulnaris	Ext. carpi ulnaris
13. Ext. secundi internodii pollicis et extensor indicis	Ext. secundii internodii pollicis et extensor indicis	Ext. secundii internodii pollicis et extensor indicis	Ext. pollicis et indicis	Ext. indicis et pollicis longus
14. Ext. ossis metacarpi pollicis	Ext. ossis metacarpi pollicis	Ext. ossis metacarpi pollicis	Ext. ossis metacarpi pollicis (Ext. pollicis brevis)	Abductor pollicis longus
15. Ext. carpi radialis	Ext. carpi radialis	Ext. carpi radialis	Ext. carpi radialis	Ext. carpi radialis
16. Flexores breves	Flexores breves	"None"	"None"	Flexores breves
17. (Not mentioned)	Adductor pollicis	"None"	"None"	"Not found"
18. Interossei dorsales	(Not mentioned)	"None"	"None"	"Not found"

relatively smaller muscle. The proximal head originates exactly as in *Neürotrichus*; the distal head originates only from the tip of the dorsal half of the proximal crest of the olecranon in company with the origin of the M. extensor indicis et pollicis longus and the insertion of the M. anconeus externus; these three muscles are not readily separable in this region. The common tendon of the two heads run distally with the tendon of the M. extensor carpi ulnaris and through a small transverse ligament on the distal end of the ulna, lateral to the transverse ligament of the wrist. Only the tendons of these two muscles pass through this small transverse ligament. The tendon of the M. extensor digiti quinti proprius then inserts into the dorsolateral angles of the proximal ends of the first and second phalanges of digit V.

Innervation. N. radialis.

Action. In *Sorex* and *Neürotrichus* the muscle is an extensor and abductor of digits IV and V, in *Scapanus* it serves digit V only.

Discussion. In *Crocidura*, according to Ärnbäck-Christie-Linde (1907), this muscle and the M. extensor digitorum communis are not separable at their origins, and she described them as a compound muscle, the M. extensores digitorum communis et digiti minimi. Dobson (1883: 153) reported the same as being true for *Desmana*. No tendency toward such a condition exists in any soricoid dissected by me. In *Neürotrichus* and *Sorex* the two tendons of insertion of the M. extensor digiti quinti proprius are readily separable, but the muscle itself will not separate into individual heads.

As stated, *Scapanus* has lost the tendon of insertion to digit IV; Dobson (1883: 167) recorded what may be an intermediate condition in *Condylura*, where a slip from the tendon of the M. extensor digiti quinti proprius passes medially and joins the tendon to digit IV of the M. extensor digitorum communis. Interestingly enough, the M. extensor carpi ulnaris inserts on digit IV in *Scapanus* (see the discussion of this muscle); the interrelationships of the changes in these insertions are not understood.

Edwards (1937), describing *Scalopus*, failed to separate the M. extensor digiti quinti proprius from the M. extensor carpi ulnaris; the latter name he assigned to both. The name "extensor quinti digiti proprius" he gave to that part of the M. extensor digitorum communis which inserts on digit V. After dissecting the extensor musculature of a single forearm of *Mogera*, I can better understand Edward's usage, if *Scalopus* resembles *Mogera*. In the latter a single muscle, which represens the M. extensor carpi ulnaris and the condyloid head of the M. extensor digiti quinti proprius, passes distally and gives off two tendons, of which the superficial passes to digit V and the deeper passes to digit IV in exactly the manner that the separate carpi ulnaris and digiti insert in *Scapanus*. The ulnar head of the M. digiti quinti proprius was absent in the single forearm of *Mogera* dissected by me.

If it were not for the exact resemblance of the double head of origin of the M. extensor digiti quinti proprius in *Scapanus* to the muscle with the same name in *Neürotrichus*, one might well call this the M. extensor carpi ulnaris, since it passes to digit V. However, the origin of the M. extensor carpi ulnaris, in *Scapanus*, is also identical with the origin of that same muscle in *Neürotrichus*, so that the identification as here stated is probably correct.

Howell (1936a) was inclined to the belief that the M. extensor digiti quinti proprius was a derivative of the extensor humero-dorsalis division, but admitted the possibility of an extensor humero-ulnaris derivation. Straus (1941) believed, however, that usually the muscle is from the extensor humero-ulnaris division, as here indicated, although he admits that in some forms it may be from the humero-dorsalis group.

M. extensor carpi ulnaris (figs. 30, 32, 33).—In *Sorex* this is a slender, fusiform muscle, the distal fourth of which is tendinous. It originates from the distal half of the lateral epicondyle of the humerus. The muscle extends along the lateral side of the antebrachium, under its own transverse ligament on the anterolateral angle of the distal end of the ulna, and continues to insert on the prominent tubercle at the anterolateral angle of the proximal end of the fifth metatarsal.

In *Neürotrichus* it is a wide, flat, fusiform muscle, whose origin lies immediately be-

neath that of the M. extensor digiti quinti proprius. The tendon runs lateral to the tendon of that muscle and inserts into the sesamoid capping the lateral tip of the ulnare. From here a strong ligament continues to the laterodorsal angle of the proximal end of metacarpal V.

In *Scapanus* the origin of this muscle is from the total length of the lateral epicondyle immediately beneath the origin of the condylar head of the M. extensor digiti quinti proprius. The tendons of these two muscles run distally within a single connective tissue sheath, but are readily separated. After running under a small transverse ligament on the distal end of the ulna, the tendon of the M. extensor carpi ulnaris continues down the lateral side of digit IV, runs beneath the tendon of the M. extensor digitorum communis to digit V, and inserts into the lateral side of the second phalanx of digit IV.

Innervation. N. radialis.

Action. In *Sorex* and *Neürotrichus*, extensor of the manus and particularly of digit V; strengthens the manus against strains acting from the lateral side. In *Scapanus*, extensor of digit IV.

Discussion. The insertion of this muscle in *Scapanus* is diffiuclt to explain; I can only suggest that in an ancestor of *Scapanus* the tendons of insertion of the Mm. extensores digiti quinti proprius and carpi ulnaris fused and then later separated in such a way that the M. extensor carpi ulnaris took over the tendon to digit IV, which had originally belonged to the M. extensor digiti quinti proprius. The alternate hypothesis is to imagine that all of the following events transpired: the origins of the Mm. extensores digiti quinti proprius and carpi ulnaris exchanged places completely and exactly; that the insertion of the M. extensor carpi ulnaris shifted down digit V from the metacarpal to the distal phalanx; and that the M. extensor digiti quinti proprius lost its tendon of origin to digit V and retained that to digit IV, thus becoming a M. extensor digiti quarti proprius. I cannot accept this hypothesis, due to the necessity of postulating a total exchange of position of origins.

If one were to dissect only *Scapanus* he would be extremely puzzled as to the proper identity of this muscle, but after tracing the extensor musculature through a soricoid series I am convinced that this muscle is properly identified.

Edward's treatment (1937) of this muscle in *Scalopus* has been discussed (p. 646). In *Condylura*, according to Dobson (1883: 169), the M. extensor carpi ulnaris arises completely from the ulna and inserts into metacarpal V; this description is so at variance with the condition as found by me in *Scapanus* that I cannot account for it.

DORSAL (EXTENSOR) DIVISION, ANTEBRACHIAL-MANUAL (DORSAL PODIAL) MATRIX, ULNO-CARPAL (ANTEBRACHIAL) GROUP

The dorsal podial extensor muscles bridged the wrist-joint in primitive tetrapods, and usually still do. Of these, the ones whose origins have moved more proximally are termed the antebrachial group.

M. extensor indicis et pollicis longus (figs. 32, 33).—In *Sorex* this is a slender fusiform muscle, of which the distal half is tendinous. It originates from the lateral half of the proximal crest of the elocranon. The tendon passes deep to all the extensors of the digits, through the transverse ligament of the wrist, and divides into three tendons upon the medial side of the dorsal surface of the carpus. At the point of division the tendon is held medially in position by a fibrous band which originates on the median side of the proximal end of metacarpal I. Of the three tendons the most median inserts upon the anteroproximal angle of the distal phalanx of digit I, the middle one inserts upon the distal phalanx of digit II, and the most lateral tendon, after fusing with a tendon of the M. extensor digitorum communis, inserts in common with that tendon into the distal phalanx of digit III.

In *Neürotrichus* this small fusiform muscle is thin but long. It originates from the dorsal half of the proximal crest of the olecranon and the adjoining posterior crest of the ulna. The muscle runs distally, superficial to the M. adductor pollicis longus, but deep to

all other muscles on the lateral surface of the ulna. After running through the transverse ligament it turns sharply mediad and divides into two tendons. The medial of these inserts upon the distal phalanx of the pollex, the lateral fuses with the tendon of the M. digitorum communis to digit II.

In *Scapanus* the origin and course of this muscle are as in *Neürotrichus*. The tendon does not divide and inserts only into the lateral side of the distal phalanx of the pollex.

Innervation. N. radialis.

Action. Extensor of digits I, II, and III and adductor of digits I and II in *Sorex;* extensor and adductor of digits I and II in *Neürotrichus* and of digit I in *Scapanus*.

Discussion. In *Crocidura* (Ärnbäck-Christie-Linde, 1907) there is no tendon to digit III, and no fusion of tendons between this muscle and the M. extensor digitorum communis. The muscle has been described as inserting upon both digits I and II in *Condylura* (Dobson, 1883: 169) and *Scalopus* (Edwards, 1937), as it does in *Neürotrichus* and *Desmana* (Dobson, 1883: 153). However, in four forearms of *Scapanus* dissected by me the muscle always had but a single slip of insertion, upon the pollex. In the single forearm of *Mogera* dissected by me the tendon split into three parts at the level of the metacarpals; of these, two inserted upon digit II and one upon digit I.

According to Straus (1941) the deep extensors of the forearm are divided into two muscles, a M. extensor pollicis longus to the pollex only, and a M. extensor proprius, which can be distributed to digits II, III, IV, and V in any combination. In the soricoids, however, the two muscles are fused, as they are in the tarsioids and the platyrrhine anthropoids (Straus, 1941), and they are consequently described here as a single muscle. If one were to dissect *Scapanus* alone, one would think that the M. extensor proprius had been lost, but the conditions in other soricoids indicate that *Scapanus* is peculiar in having the two muscles present and fused with a single tendon to the pollex only.

M. abductor pollicis longus (figs. 32, 33).—In *Sorex* this muscle originates from the lateral half of the proximal crest of the olecranon and from the lateral surface of the olecranon. The muscle extends down the proximal antebrachium in the groove between the radius and ulna and continues as a tendon which then crosses the forearm obliquely, on the anterior side from lateral to medial, superficial to the tendon of the M. extensor carpi radialis but deep to the tendons of the other extensor muscles. The tendon runs through a groove on the anteromedial angle of the distal end of the radius and inserts into the process on the anteromedial angle of the proximal end of metacarpal I.

In *Neürotrichus* the relationships and insertion of this muscle are as in *Sorex*, but the origin consists of two heads. The radial head originates from the dorsal surface of the capitular process. The ulnar head is again divided into two; the more superficial of these arises from the posterior crest of the ulna immediately superficial to the insertion of the M. anconeus externus, and the deep portion arises from the whole of the fossa between the semilunar notch and the posterior crest, deep to the insertion of the M. anconeus externus. The two ulnar heads unite immediately, cross the rim of the head of the radius as a thick bundle, and unite with the radial head one-third of the distance distally of the length of the radius.

In *Scapanus* the origin and insertion of this muscle are exactly as in *Neürotrichus*. The dorsal surface of the radius is deeply grooved where the tendon crosses it.

Innervation. N. radialis.

Action. Abductor of the pollex.

Discussion. Ärnbäck-Christie-Linde (1907) described this muscle in *Crocidura* as having part of the origin on the radius and interosseous septum and inserting partially upon the carpus; none of these statements would be true for *Sorex*.

APPENDICULAR SYSTEM (PECTORAL LIMB), VENTRAL (FLEXOR) DIVISION, ELBOW MATRIX, ANTEBRACHIAL GROUP

Howell (1936a) and Straus (1942) divided these antebrachial flexors of the elbow into three groups: humero-radialis (radial marginal), humero-palmaris (intermediate), and humero-ulnaris (ulnar marginal).

FLEXOR HUMERO-RADIALIS DIVISION

M. pronator radii teres (figs. 30, 32, 33).—In *Sorex* this is the most proximal muscle to have its origin from the median epicondyle. The muscle runs distally and curves slightly to insert upon the anterior surface of the radius, immediately proximal to the midpoint of the length of the radius.

In *Neürotrichus* this is a large and powerful muscle which arises from the medial epicondyle and the medial supracondyloid ridge of the humerus, runs distally, and inserts along the pollical-palmar surface of the second fourth of the radius.

In *Scapanus* this is the largest muscle in the forearm, except for the Mm. flexor digitorum profundus and extensor digitorum communis; even the M. biceps brachii is smaller than the M. pronator radii teres. The origin is from the whole of the anterior side of the medial epicondyle, deep to the M. palmaris longus and proximal to the origin of the great profundus ligament. The muscle curves but slightly in passing around the pollical edge of the ulna to insert distally to the insertion of the M. biceps brachii upon the whole of the pollical surface of the middle third of the radius. Part of the insertion is fused with a part of the insertion of the M. biceps brachii.

Innervation. N. medianis.

Action. This muscle has come to be a flexor of the forearm in the talpids, but there must be some function it serves other than this to explain its great hypertrophy in the more fossorial forms. What this function might be is not understood.

M. flexor carpi radialis (fig. 32).—In *Sorex* this is a relatively large fusiform muscle which originates superficially from the anterior surface of the proximal part of the medial epicondyle, between the origins of the M. pronator radii teres and the condylo-radialis head of the M. flexor digitorum profundus. The M. flexor carpi radialis lies superficial to the union of the radialis proprius and condylo-radialis heads of the profundus, but further distally the tendon hugs the bone and comes to lie in the groove between radius and ulna on the posterior side of the antebrachium. Into this groove it is bound by heavy connective tissue and, passing deep to the common tendon of the profundus, it inserts upon the proximal part of the palmar surface of metacarpal III.

Dobson's description of this muscle in *Desmana* (1883: 154) fits *Neürotrichus* perfectly: ". . . arises from the internal condyle under cover of the palmaris and between the large tendon of the flexor profundus and the pronator radii teres and is inserted into the second metacarpal bone." The tendon passes deep to the profundus tendon and then through a groove between the intermedium and the centrale, to reach its insertion.

In *Scapanus* the muscle originates on the anterior surface of the humerus between the trochlea and the pit for the origin of the great profundus ligament; the origin is thus more distal than in the other two genera. The tendon of the muscle runs distally, completely circling the median nerve, and passes to the palm deep to the M. flexor digitorum profundus to insert into the connective tissue between metacarpals II and III.

Innervation. N. medianis.

Action. Flexor of the hand upon the wrist. The muscle in *Scapanus* is so small in relation to the size of the hand that it does not seem possible that it could have any effect

Discussion. In *Sorex* the tendon of insertion contains a sesamoid at the level of carpale III; this sesamoid is not found in the other two genera.

FLEXOR HUMERO-PALMARIS DIVISION

M. palmaris longus (figs. 30, 32).—In *Sorex* this is the most superficial muscle on the median side of the antebrachium. It is a medium-sized fusiform muscle, and the distal half is a thin tendon. It originates from the tip of the median epicondyle of the humerus and the thin tendon runs distally with the larger tendon of the M. flexor carpi ulnaris and then broadens out to run superficially to it. The broadened tendon crosses the pisiform and spreads out into the superficial fascia of the palm, where part of it inserts into the lateral of the two large carpal pads; a major portion continues beyond as a definite

tendon which inserts upon the second phalanx of digit V in the exact manner as does each tendon of the M. flexor digitorum sublimus into its digit.

In *Neürotrichus* this muscle differs remarkably from the condition in *Sorex* in that it has a double insertion. It originates in the same manner, from the tip of the medial epicondyle of the humerus, but the distal end of the muscle gives off two tendons. These run, respectively, to the palmar surface of the first and fifth fingers and insert particularly upon the distal phalanges, although both anastomose also with the general palmar fascia. The tendon to digit I, as it crosses the radiale, contains a small sesamoid, which I interpret as the homologue of the falciform bone in *Scapanus*. The tendons of the M. flexor digitorum profundus to digits I and V do not perforate the tendons of the M. palmaris longus to those same digits, as the profundus tendon does the palmaris tendon in *Sorex*.

In *Scapanus* the muscle is as in *Neürotrichus*, but the muscular part is broader and shorter; of the two tendons, the minimal inserts on digit V as in *Neürotrichus*, but the pollical inserts directly upon the proximopalmar angle of the falciform bone. Connective tissue between the falciform bone and the medial side of the pollex and between the tendon of the palmaris and the medial side of the pollex would transmit the force of contraction of the palmaris to the pollex.

Innervation. The innervation of this muscle in *Scapanus* is interesting, inasmuch as the muscle receives two twigs from the median nerve, one around each side of the great ligament of the M. flexor digitorum profundus; the deeper of these two nerves receives a few fibers from the N. ulnaris. The double arrangement of the nerves to this muscle would suggest a double muscle in *Scapanus* (and presumably also in *Neürotrichus*), a conclusion strengthened by the presence of two tendons and two insertions.

Action. In *Sorex* the muscle tightens the fascia and skin of the palm and at the same time is a flexor of the hand at the wrist; the distal continuation of the tendon serves as a special flexor of digit V. In *Neürotrichus* the muscle is a flexor and abductor of digits I and V, and thus strengthens and broadens the hand in the digging stroke. In *Scapanus* the muscle is a flexor of digit V and an abductor of digits I and V; it also rotates the falciform bone so that its greatest width lies in the same plane as does the palm of the hand. In *Scapanus*, therefore, the muscle is even more of an aid during the digging stroke than it is in *Neürotrichus*.

Discussion. In *Crocidura* (Ärnbäck-Christie-Linde, 1907) the M. palmaris longus is similar to that of *Sorex* in general configuration except that the distal tendon to the fifth finger is not tendinous, but muscular; she named it the M. flexor brevis digitorum manus. The tendon of insertion of this short muscle is perforated by the tendon of insertion of the M. flexor digitorum profundus, as is the tendon of the M. palmaris longus in *Sorex*. It would seem, then, that the tendon of the palmaris, which normally inserts into the palmar fascia (as it does partially in *Crocidura* and *Sorex*), has become the site of origin of an intrinsic muscle of the hand, probably the M. abductor digiti quinti; in *Crocidura* this muscle is still present, but in *Sorex* it has become completely tendinous, and it is retained in its tendinous state in *Neürotichus* and *Scapanus*.

Desmana and *Condylura* (Dobson, 1883: 153, 169), and *Scalopus* (Edwards, 1937) resemble *Neürotrichus* and *Scapanus* in the configuration of the M. palmaris longus.

Straus (1942) and Howell (1936a) do not agree as to the phylogenetic history of this muscle; here I have tentatively followed Straus, as the most recent author, and assigned it to the intermediate (palmaris) division of the antebrachial flexors of the elbow matrix. Howell was of the opinion that the M. palmaris longus can arise from the radial marginal or the ulnar marginal divisions of the antebrachial flexors, or from both. The evidence as found in *Neürotrichus* and *Scapanus* would seem to indicate a dual origin for this muscle, as Howell has suggested is possible. If this is true the M. palmaris longus in the talpids has been derived by a fusion of radial marginal and ulnar marginal components, which have maintained their tendons intact. The situation in *Crocidura* and *Sorex* could then be explained either by a loss of the radial tendon or of the radial marginal head of the muscle.

M. flexor digitorum sublimus (figs. 30-33).—The three heads of this muscle in mam-

mals are commonly called condylo-radialis, centralis, and condylo-ulnaris, a usage which will be followed here, although I am fully aware that these names are of topographic convenience only and do not indicate homologies, as discussed by Howell (1936a). The muscles are different in the three genera dissected and each genus will be described separately, *Sorex* first.

Condylo-ulnaris head: This muscle consists of a few short fibers and a long tendon; it originates from the distal surface of the medial epicondyle deep to the centralis head and proximal to the centralis portion of the M. flexor digitorum profundus. The tendon passes in a separate tunnel through the medial part of the transverse carpal ligament and continues to digit II. At the distal end of metacarpal II the tendon divides into two; of these the lateral passes exterior to the proximal annular ligament, passes laterally around the tendon of the M. flexor digitorum profundus of digit II, and then beneath that tendon. The medial of the two tendons of the condylo-ulnaris head of the sublimus passes through the proximal annular ligament in company with the tendon of the M. flexor digitorum profundus, and then passes medially around the tendon. On the deep side of the profundus tendon these two fuse into one tendon again, and inserts into the palmar edge of the second phalanx of digit II.

Centralis head: This portion is somewhat larger, and the muscular part is longer, than the preceding; it originates from the medial epicodyle immediately proximal to the first part and the tendon runs distally to penetrate a separate tunnel through the middle part of the transverse carpal ligament. It inserts into digits III in the same way as does the condylo-ulnaris head of digit II.

Condylo-radialis head: This is a thin muscle, but as long as the preceding. It originates deep from the anterior surface of the medial epicondyle, between the origins of the heads centralis and condylo-radialis of the M. flexor digitorum profundus. The tendon passes distally and through a separate tunnel through the lateral part of the transverse carpal ligament. It inserts upon digit IV as did the condylo-ulnaris head upon digit II.

In *Neürotrichus* there are also three separate muscles representing the M. flexor digitorum sublimus, but the positions of the origins have shifted considerably; they would be difficult to name except that the three tendons insert as in *Sorex*.

Condylo-ulnaris: The origin of this head is from the distal portion of the posterior surface of the medial epicondyle, deep to the origin of the M. epitrochleo-anconeus. The muscle lies superficial to the origin of the other two communis heads and superficial to the origin of the centralis head of the profundus. The small tendon emerges from between the great ligament of the profundus and the condylo-ulnaris head of the profundus; here it runs superficially to the great ligament and, at the level of metacarpal II, is perforated by the tendon of the profundus to digit II. Insertion is upon the palmarproximal edge of the first phalanx of digit II.

Centralis: The small head of this muscle originates from the medial side of the distal portion of the coronoid fossa and becomes tendinous almost immediately. The tendon circles the ulnar side of the great profundus ligament to insert upon digit III as the condylo-ulnaris head inserts on digit II.

Condylo-radialis: This small muscle is again subdivided into two heads, which originate side by side from the lateral half of the distal part of the coronoid fossa. The two tendons together pass around the ulnar side of the great profundus ligament and unite at the level of the wrist. The single tendon is perforated by the tendon of the profundus to digit IV and then inserts upon digit IV as did the tendon of the condylo-ulnaris head upon digit II.

In *Scapanus* there is but a single head of this muscle; its homology in *Sorex* and *Neürotrichus* cannnot be determined. Origin is from the medial epicondyle at the medial edge of the point of origin of the great profundus ligament and from the ulnar border of the proximal fourth of that ligament. The flat tendon curves around the ulnar border of the

great ligament of the profundus onto the superficial surface of the palm, where it fuses with the connective tissue accompanying the palmar branches of the median nerve, and together they are distributed to the four interdigital spaces. These ultimate tendons merge with the heavy connective tissue of the interdigital spaces and could not be traced to any definite insertions.

Innervation. I was unable to find the innervation of the different heads of this muscle in *Sorex* or *Neürotrichus;* the single head of *Scapanus* is innervated by the median nerve.

Action. The muscle in *Sorex* and *Neürotrichus* is a flexor of digits II-IV, and a flexor of the hand at the wrist; in *Scapanus* it is a flexor of the hand only. In the two fossorial genera the muscle is so small as to have little functional importance; flexion of the fingers is accomplished primarily by the great ligament of the profundus.

Discussion. The presence in *Sorex* of a sublimus-type tendon to digit V has been discussed in connection with the M. palmaris longus. In *Sorex* the origins of this muscle are not fused with the origins of parts of the M. flexor digitorum profundus, as described for *Crocidura* (Ärnbäck-Christie-Linde, 1907). Dobson's descriptions (1883) of the sublimus in *Desmana* and *Condylura* are not complete enough to allow comparisons. I am of the opinion that the muscle in *Scalopus* termed by Edwards (1937) the "M. flexor digitorum sublimus" is in reality a head of the profundus, and that he missed the sublimus entirely.

Although the M. flexor digitorum sublimus has here been discussed with the antebrachial flexors of the elbow and is thus considered as a part of the superficial musculature of the forearm, it should be pointed out that extensive transfers of muscular tissue between deep and superficial layers have occurred in this region, a fact noted as long ago as 1889 by Windle. Indeed Howell (1936a) and Straus (1942) present evidence to show that the profundus and sublimus flexors were fused in primitive mammals and have subsequently separated again, but not always along the original line of fusion.

FLEXOR HUMERO-ULNARIS DIVISION

M. epitrohleo-anconeus (figs. 31, 32, 34).—In *Sorex* this is a short but sturdy muscle which originates from the tip of the medial epicondyle of the humerus and inserts along the medial side of the olecranon. In *Neürotrichus* and *Scapanus* the muscle is the same, except that it is larger and longer, in correlation with the increased size and length of the osseous processes to which it attaches. In *Scapanus* there is a second head of origin from the fossa on the posterior surface of the humerus lying between the trochlea and the elevation that marks the origin of the great ligament of the profundus.

Innervation. By N. ulnaris in all three genera; both heads in *Scapanus* are innervated by the ulnar nerve. Edwards stated that the muscle in *Scalopus* occupying this position is innervated by the radial nerve, and therefore he calls the muscle an anconeus medialis; I tried particularly in several specimens of each genus dissected by me to trace a twig of the radial nerve into this muscle, but was unable to do so. In each example I found, instead, one or more small twigs from the ulnar nerve entering the muscle.

Action. The action of this muscle is problematical, although it is usually termed an extensor of the forearm. However, in *Neürotrichus* and *Scapanus*, which possesses long olecranon processes, the muscle is almost parallel with the long axis of the ulna, no matter what the position of that bone may be. Under these circumstances the muscle would seem to serve no other purpose than to draw the ulna distally and against the capitulum. The great increase in size of the muscle of *Neürotrichus* over *Sorex* and of *Scapanus* over *Neürotrichus* would suggest, however that the muscle does possess an extensor function and has hypertrophied to approximately the same degree as has the M. triceps.

M. flexor carpi ulnaris (figs. 30, 32, 34).—In *Sorex* this wide, fusiform muscle is the most superficial on the posterior surface of the antebrachium. It originates from the proximal tip of the posterior surface of the olecranon. The insertion is upon the pisiform bone; a stout ligament between the pisiform bone and the proximal edge of metacarpal V transmits the movement to the latter bone.

In *Neürotrichus* the muscle is narrower, but with a larger belly than in *Sorex*. Origin is by two heads, one from the medial epicondyle of the humerus, deep to the origin of the M. palmaris longus; the other head originates from the minimal side of the proximal crest of the olecranon. The two heads fuse to a common tendon, which inserts as in *Sorex*.

In *Scapanus* the origin is as in *Sorex* (the humeral head of *Neürotrichus* is missing); insertion is on the pisiform, but contraction of the muscle on the medial edge of the pisiform rotates that bone on its central axis, so that the lateral side is thrown distally, thus relaxing the tendon which runs to the fifth metacarpal.

Innervation. N. ulnaris.

Action. In *Sorex* and *Neürotrichus* a general flexor of the hand and a special flexor of metacarpal V. In *Scapanus* the muscle is also a general flexor of the hand, but relaxes the ligament to metacarpal V; this latter action is not understood.

Discussion. Ärnbäck-Christie-Linde (1907) described a head of origin from the internal condyle in *Crocidura*, as I found in *Neürotrichus*, but in none of the soricoids dissected by me is there a partial fusion of this muscle with the M. palmaris longus, as she also described for *Crocidura*. The origin is double in *Desmana* (Dobson, 1883: 154) and thus comparable to *Neürotrichus*, but from the ulna alone in *Condylura* (Dobson, p. 169) and *Scalopus* (Edwards, 1937).

VENTRAL (FLEXOR) DIVISION, WRIST (ANTEBRACHIO-MANUAL) MATRIX, ANTEBRACHIAL GROUP

These are muscles which primitively were flexors across the wrist-joint, but whose origins have moved proximally, deep to those antebrachial flexors which were derived from the elbow-joint and whose insertions migrated distally.

M. pronator quadratus (fig. 34).—This muscle has not heretofore been described in any soricoid, presumably due to its small size, but I found it in *Sorex* and *Neürotrichus*.

Usually the muscle is described as originating on the ulna and inserting on the radius, but in Sorex the fibers run obliquely and distally from radius to ulna. The origin is upon the anterior surface of the proximal third of the radius; the short fibers run obliquely forward in a thin sheet to insert upon the posteriomedial angle of the shaft of the ulna.

In *Neürotrichus* the muscle is short, flat, and narrow, but larger in actual size than in *Sorex*. In both genera the positive identification of cross-striations of the muscle fibers, using a compound microscope, proved the transparent interosseous septum to be muscular.

The innervation of this small muscle was not determined.

Action. The muscle is presumably degenerating in the Soricoidea; in any case it could have no possible action, both because of its small size and because of the impossibility of pronation in *Sorex* and *Neürotrichus*.

M. flexor digitorum profundus (figs. 30-32, 34).—As discussed by Windle (1889), this muscle usually consists of five heads in mammals; Windle's terminology for these heads will be followed here. Howell (1936a) has pointed out, however, that these heads are not fundamental, but that fibers shift back and forth readily between them; moreover there may be transfer of fibers with those of the sublimus, so that Windle's names are of topographic convenience only. Each genus will be discussed separately, beginning with *Sorex*.

1. *Ulnaris proprius:* The origin of this head is the deepest on the medial surface of the olecranon. It is a large, fusiform muscle, of which the distal half is tendinous.

2. *Condylo-ulnaris:* This is a small fusiform muscle with a shorter belly than the preceding. It originates from the distal end of the medial surface of the medial condyle of the humerus, runs distally with the M. ulnaris proprius, and is covered by the lateral head of the M. flexor digitorum sublimus.

3. *Centralis:* This is the smallest and shortest of the five heads. Its origin lies deep to that of the condylo-ulnaris head of the sublimus and springs from the groove between medial epicondyle and medial condyle.

4. *Condylo-radialis:* Next to the ulnaris proprius, this is the largest head. It originates from the anterior face of the medial epicondyle, between the origins of the M. flexor carpi radialis and the condylo-radialis head of the sublimus. There is no origin from the radius. The muscular belly runs almost half the length of the antebrachium and is fused distally with the belly of the radialis proprius.

5. *Radialis proprius:* Next to the centralis, this is the smallest head. It originates from the proximal fifth or sixth of the medial surface of the radius and, about one-third distad on the antebrachium, its belly fuses with that of the condylo-radialis.

Insertion: The radialis proprius and condylo-radialis have one large tendon in common; the tendons of the other three heads join this one and each other at the distal end of the antebrachium. The common tendon passes beneath the transverse carpal ligament, deep to the tendons of the M. flexor digitorum sublimus, which pass individually through that ligament. Beyond the carpus the common tendon of the profundus divides into five again; each of these continues onto a digit, passes through two annular ligaments and inserts into the distal phalanx of its digits. All of the tendons of insertion except those of digits I and V give off small medial and lateral tendons which insert with tendons of the M. flexor digitorum sublimus, the tendons of insertion of which are perforated, respectively, by the tendons of insertion of the profundus to digits II, III, and IV.

The tendon to digit V perforates the tendon of insertion of the M. palmarus longus (p. 650).

A flat ligament from carpale IV + V (hamatum) runs transversely deep to the common profundus tendon and inserts upon its medial side, serving to hold it in place; a similar ligament was found in *Crocidura* by Arnbäck-Christie-Linde (1907), who described but four heads of origin for the profundus in *Crocidura*. I think that she considered the radialis proprius and the condylo-radialis as one head.

In *Neürotrichus* this muscle also consists of five heads, plus a great non-muscular ligament. This ligament originates from the pit on the distal tip of the medial epicondyle of the humerus (fig. 5), and the tendons of all the muscular bellies join it. These bellies will be described in the same order as in *Sorex*, but they are not necessarily completely homologous.

1. *Ulnaris proprius:* The origin of this muscle is deep upon the palmar side of the proximal crest of the olecranon. The tendon runs distally, beneath that of the M. flexor carpi ulnaris, crosses the tendon of the condylo-ulnaris head of the profundus, and joins the common ligament at the level of the wrist. The fibers, if followed, go to digits II, III, and IV.

2. *Condylo-ulnaris:* The origin of this muscle in *Neürotrichus* is not condylar, but lies upon the palmar surface of the olecranon proximal to the head of origin of the ulnaris proprius. The long, slim muscle becomes tendinous somewhat distal to the elbow; this tendon runs deep to the great ligament of the profundus and doe not join it until in the palm of the hand. The fibers, if followed, run only to digits I and II.

3. *Centralis:* This small head originates from the fossa on the medial side of the trochlea on the posterior surface of the humerus. The muscle runs distally a short distance and its tiny tendon merges with the great ligament.

4. *Condylo-radialis:* The origin of this muscle lies along the radial border of the ulna immediately distal to the coronoid process. The fibers run distally, parallel with the ulna, and unite with the fibers of the radialis proprius immediately distal to the insertion of the M. biceps brachii. The short, common tendon of these two heads then joins the great communis ligament on its pollical side. The tendon of the M. brachialis, where it inserts upon the radius, separates the origin of the condylo-radialis head from

the three heads previously described, from the great ligament of the profundus, and from the three heads of the M. flexor digitorum sublimus.

5. *Radialis proprius:* This is a small triangular muscle with a wide area of origin upon the palmar surface of the proximal sixth of the radius. The distal, narrower portion of the fleshy belly joins the condylo-radialis, and their short, common tendon merges with the great ligament of the profundus. Proximally the muscle is separated from the origin of the condylo-radialis by the tendon of insertion of the M. biceps brachii.

Insertion: The common tendon of the great ligament and the five muscular heads passes onto the palm (there is no transverse carpal ligament of the palmar surface in *Neürotrichus*); at the level of the palm the common tendon contains within itself a large sesamoid. The tendon then divides into five, each of which continues out a digit and inserts into the distal phalanx after running beneath several annular ligaments (not all shown in figure 32). The tendons to digits II, III, and IV perforate the sublimus tendons to those same digits.

In *Scapanus* the great ligament of the profundus originates and courses as in *Neürotrichus*, but is relatively much larger; it is as broad and thick as is the shaft of the ulna. There are but three muscular heads present; two of these are so small and so crowded that no attempt can be made properly to indentify them.

The first head, which appears to correspond to the ulnaris proprius of *Sorex* and *Neürotrichus*, originates deep from the whole palmar surface of the olecranon and the proximal half of the ulnar shaft. The flat tendon crosses onto the superficial surface of the great ligament on its ulnar side and fuses with the ligament at the level of the carpus. The fibers can be traced to all five digits. It is this muscle which Edwards (1937) erroneously termed the M. flexor digitorum sublimus in *Scalopus*.

The second head, which may correspond to the centralis, is small and originates from the distal end of the medial epicondyle, immediately deep to the origin of the great ligament. The muscle runs parallel with the ligament and joins it by a small tendon which can be traced within the ligament as a separate round bundle to the level of the metacarpals.

The third head lies deep to the first, and originates along the shaft of the ulna from the coronoid process to the distal third of the ulna. The fibers aggregate to a flat tendon which merges immediately with the great ligament on its deep surface.

At the level of the metacarpals the common tendon divides into five, one of which inserts upon the distal phalanx of each digit.

The innervation was determined only in *Scapanus*, where the first head (ulnaris proprius?) is innervated by the ulnar nerve; the other two heads and the great ligament receive branches from the median nerve.

Action. In *Sorex* this muscle is a simple flexor of the digits by contraction of the muscle. In *Neürotrichus* and *Scapanus*, however, the muscular heads decrease in size with increase in fossorial activity, until in *Scapanus* the muscular heads are so small in proportion to the size of the hand and the work it does that it is obvious that the muscle cannot perform its functions solely by contraction. This condition was first pointed out by Thompson (1884) for *Talpa*, but is true of every talpid ever described. Thompson also accurately explained the action of this ligament, but his paper has generally gone unnoticed except for a reference to it by Freeman (1886).

The following is a summary of Thompson's explanation of the action of this ligament, an explanation I find to be correct. In *Talpa* and other talpids the ligament originates from the medial side of the humerus, whereas the capitulum and trochlea lie upon and toward the lateral side, respectively. There is thus quite a gap between the point of attachment of the ligament and the points of contact of the radius and ulna with the humerus. When the true medial edge of the humerus is not rotated posteriorly, the tendon is in a relaxed state and the fingers can be extended. As the medial edge of the humerus is rotated posteriorly by the action of the Mm. teres major, latissimus dorsi,

subscapularis, and pectoralis superficialis posticus, the lever arm of the antebrachium and manus is also swung in a horizontal circle laterally and then posteriorly because the great ligament of the profundus, running from the medial epicondyle to the digits, pulls that lever arm posteriorly. The fingers are not actually flexed, because of the resistance of the earth against them; indeed, the resistance of the earth keeps them almost extended, but the power of the pull transmitted through the ligament drags them through the soil.

The truth of this explanation was tested on a half-grown mole freshly killed and skinned; on a fresh animal of this type one can manipulate the parts with ease. By placing one's finger tip in the palm of the mole's hand, to simulate the resistance of the earth, and then rotating the humerus of the mole manually, the great ligament could be felt to tighten immediately and the digits would close around the tip of one's finger; as the humerus was further rotated the force against one's finger increased and clearly demonstrated the manner in which the rotation of the humerus is transmitted to the forearm and hand.

If it were not for some such compensatory ligament originating from the medial edge of the humerus and assuming most of the burden of the transfer of humeral rotation to the hand the force of the rotation of the humerus and the opposing force of the earth against the hand would meet at the elbow and break the joint.

Discussion. The determination of the homology of the great ligament of the talpids with any structure in *Sorex* is not possible on the basis of evidence at hand. Since the three heads of the sublimus and the five heads of the profundus are present in both *Sorex* and *Neürotrichus*, the great ligament probably could not have been derived from a muscular head, although as Howell (1936a) has mentioned, the profundus and sublimus heads may have various degrees of fusion and separation in different groups of mammals, so that the great ligament could represent a structural combination not found in other mammals; this new head could have subsequently become ligamentous. Or the great ligament may merely represent an aggregation of forearm fascia which originally lay in the region between the medial epicondyle and the primitive profundus tendon; subsequent strengthening of this fascial bundle could then enlarge this structure to the size it has attained in the talpids.

WRIST (ANTEBRACHIAL) MATRIX

PODIAL GROUP

These are muscles which bridged the wrist in primitive tetrapods, but have moved distally upon the hand. Howell (1936a) divided them into superficial and deep sets. In the soricoids the only possible representative of the superficial set present is the M. abductor digiti quinti, which has been discussed with the M. palmaris longus (p. 650). The remainder are deep flexors of the manus.

Mm. flexores breves.—In *Sorex* there are ten of these muscles, a lateral and a medial one for each digit. McMurrich (1903), although he never made an outright statement, inferred that the basic arrangement for each of these muscles would be with the origin on the side of the metacarpal and insertion on the same side of the first phalanx of the same digit. If this is the primitive pattern, *Sorex* has retained it with but few changes.

The muscles for digit II and the lateral pollical flexor originate from the respective palmar surfaces of their metacarpals, as they primitively should. The muscles for digits III and IV and for the medial side of digit V originate by a strong, common tendon from carpales III and IV + V (hamatum). The muscle for the lateral side of digit V originates from the distal tip of the pisiform. The muscle for the medial side of the pollex originates from the tip of the prominent process on the palmar side of the radiale portion of the scapholunar bone.

At its distal end each muscle, with the exception of the medial muscle to digit V, inserts in the same way. The distal end of the muscle narrows to a tendon, which divides into two; one of these inserts upon the side of a sesamoid (of which two cover the palmar surface of the joint between metacarpal and the first phalanx), and the other

continues around the sesamoid to insert into the proximal edge of the first phalanx. The muscle on the medial side of digit V runs across the palmar surface of metacarpal V to insert with the lateral muscle of digit V; this is presumably a device to attain more powerful abduction of digit V.

In *Neürotrichus*, for digits II, III, and IV, small tendons could be found, two to a digit and occupying the normal position of the Mm. flexores breves. Identification of such structures in digits I and V was not certain. Examination of these tendinous flexores breves under the high power of a compound microscope revealed scattered muscle fibers, but these were too few to have any functional value and it is considered that the intrinsic musculature of the hand in *Neürotrichus* is in an intermediate stage of degeneracy.

Only one muscle is present in the hand of *Scapanus*, but it is well developed and seems to represent the medial flexor brevis to the pollex; it here acts as an abductor of the pollex. The muscle arises from the medial surface of the radiale and inserts on the medial side of the sesamoid which lies at the distal end of the palmar surface of metacarpal I. The muscle is necessarily short, but is thick, and from its size presumably is of value to the animal.

In the single hand of *Mogera hainana* dissected by me there was present what I presume to be the same muscle as was found in the hand of *Scapanus;* this muscle in *Mogera* originates from the distal tip of the radiale and inserts into the center of the sesamoid at the distal end of the metacarpal of the pollex. The structure was tendinous throughout with a few muscle fibers in the center; it tended to abduct the pollex when tightened, but its minute size would preclude any possibility of important action.

Innervation. Not determined.

Action. In *Sorex* these muscles act as abductors, adductors, or flexors, according to which of them are put to use. They are extremely small, but the hand of *Sorex* is delicately built and the muscles are presumably of service to the animal.

Discussion. I am using the term "flexores breves" in the sense as it has been used by Dobson (1883), McMurrich (1903), and Arnbäck-Christie-Linde (1907). Howell (1936a) applied this term only to a layer of deep podial muscles of amphibians and reptiles, and found that he could not homologize this layer exactly with any one layer of deep podial flexors in mammals. Since, however, I cannot correlate the muscles as I find them in *Sorex* with Howell's terminology, I am reverting to the usage of the older anatomists.

Not all Desmaninae lack the Mm. flexores breves, as Dobson (1883: 154) reported them present in *Desmana*, but he did not clearly state their number or arrangement. He also listed the M. adductor pollicis as being found in *Desmana*.

In *Condylura* (Dobson, 1883: 170) and *Scalopus* (Edwards, 1937) no intrinsic musculature of the hand has been found; Dobson's statement must be taken cautiously, inasmuch as he made the same claim for *Scapanus*.

Mm. interossei dorsales.—Arnbäck-Christie-Linde (1907) listed four interossei deep to the flexores breves in *Crocidura;* I found no such muscles in any soricoid I dissected.

SUMMARY OF THE MUSCULATURE OF THE FORE LIMB

The muscular action of the talpine shoulder and brachium has been analyzed previously by Freeman (1886) and Campbell (1939); in addition Thompson (1884) explained the action of the great ligament of the M. flexor digitorum profundus in the forearm of *Talpa*, but his conclusions are valid for all talpids possessing the ligament. The points of view of Freeman and Campbell differed somewhat in that the latter attempted a more mechanical approach, but their conclusions were in agreement on all major points; neither investigator, however, dissected beyond the elbow, and Thomp-

son limited himself to the discussion of the one ligament, so that a complete summary of the action of the talpid fore limb has not hitherto been attempted. Any discussion of the digging action of the fore limb will apply equally to *Scapanus* and *Neürotrichus* and generally will apply to talpines as well as to burrowing desmanines. The chief difference in the burrowing stroke is found in the degree of the strength of action.

At the beginning of the stroke the arm and hand are extended anteriorly. Extension of the humerus is accomplished by the Mm. supraspinatus and superficialis anticus (perhaps aided by the Mm. acromiodeltoideus and cleidodeltoideus). The equal and opposite resultant force is partly transmitted to the sternum, which is supported by the rib-cage, and partly to the scapula, which is held in place by the action of the Mm. serratus anterior thoracis, serratus anterior cervicis, trapezius posticus, and rhomboidei.

Extension of the antebrachium at the beginning of the digging stroke is affected by the powerful triceps complex of each side of the body. Contraction of the Mm. triceps longus would displace the scapulae laterally and dorsally, except that they are fixed by the same series of muscles as absorb the force of the extension of the humerus. Extension of the hand and digits is accomplished by the forearm extensors. In this extended position of the arm the palm of the hand necessarily faces ventrolaterally; no other position is possible because of the limiting factors inherent in the construction of each joint.

If the soil is loose the mole extends the arms and hands of both sides; a simultaneous "breast-stroke" of both arms will now pull the animal through the loose soil. If the earth is hard and the mole is constructing a deep burrow, only one arm and hand will be extended and a single posterior stroke used to scratch loose the soil. In either instance the action of the individual limb is fundamentally the same.

If the whole limb were retracted in a full arc from the extended position, the arm would simply swing posteriorly in a lateral or dorsolateral circle with the lateral (minimal) edge of the manus cutting the soil. No effective burrowing stroke would result because the hand would not lie at right angles to the direction of the movement of the arm.

Since a talpid cannot pronate the hand to turn it at right angles to undertake such a digging stroke, the humerus must be rotated instead, so that the true medial border is turned laterad. Such action, alone, will turn the palm dorsolaterally. Retraction of the humerus in this rotated position will force the palm through the soil in a dorsolateral sweep; the fingers are automatically semi-flexed by the mechanical action of rotation of the humerus transmitted through the great ligament of the M. flexor digitorum profundus.

I was able to prove satisfactorily to myself and to other observers that rotation and retraction of the humerus is the true basis of the talpid burrowing stroke. This was done by manipulation of the humerus of a freshly-

skinned, half-grown individual of *Scapanus latimanus*. Burrowing strokes could be achieved by the manipulator by following the pattern of the motion as described above, but in no other way could they be brought about.

The talpid does not perform a burrowing stroke by rotation of the humerus first, followed by retraction; the two movements are accomplished by the same group of muscles and occur simultaneously. The muscles of this group are those inserting on the true medial border of the humerus; the Mm. teres major, latissimus dorsi, subscapularis, and pectoralis superficialis posticus. These are the most hypertrophied group of muscles in the talpid body. The opposing and controlling force which determines the relative rates of rotation and retraction of the humerus is furnished by the counter-rotators, which insert on the opposite (lateral) side of the humerus. Of these the most important in this particular action probably is the M. spinodeltoideus; the M. pectoralis superficialis anticus is also a large counter-rotator, but it is more of an extensor and adductor than is the M. spinodeltoideus and would tend to negate the action of the great rotators rather than control it.

Campbell has pointed out that the contraction of the M. teres major would pull the posterior ends of the two scapulae laterally were it not for the interscapular ligament (a part of the M. rhomboideus posticus) which holds the scapulae together. In *Neürotichus*, where the M. rhomboideus posticus is not tendinous, it must contract with each digging stroke. Undoubtedly all muscles inserting upon the posterior end of the scapula aid in holding it firm during the burrowing stroke.

The hand can be broadened at any time by the Mm. abductor pollicis longus, extensor carpi ulnaris, extensor digiti quinti proprius, and palmaris longus.

Recovery from the burrowing stroke is effected by counter-rotation of the humerus and flexion of the antebrachium. Counter-rotation is accomplished by the Mm. spinodeltoideus, supraspinatus, pectoralis superficialis anticus, and infraspinatus (the latter missing in *Talpa* and *Mogera*). Flexion of the forearm is accomplished by the Mm. brachialis anticus, pronator radii teres, and biceps brachii; contraction of the latter also automatically counter-rotates the humerus (p. 642).

Presumably no talpid always makes the burrowing stroke at exactly the same level with reference to the body. Varying degrees of flexion and extension of the forearm will change the elevation of the burrowing stroke; from personal observation it is my opinion that this is the most important factor in the control of elevation. Also the talpid can theoretically depress the humerus by contraction of the Mm. pectoralis profundus (missing in *Neürotrichus*) and cleidoletoideus; such action is limited, however, by the nature of the joint between the glenoid fossa and the head of the humerus. In practice a talpid rotates in its burrow to accomplish any extensive shift in level of operation, thus demonstrating the rigidity of the pattern of action of the fore limb. *Neürotrichus*, which elevates the humerus for

burrowing or depresses it for digitigrade locomotion, probably has much greater freedom of action in changing the level of the burrowing stroke.

A complete sweep of the hand through the soil is not the only action of the fore limb in burrowing, as an important motion is the lateral thrust used in raising the roofs of the shallow runways of the talpines or in packing the soft soil into the side of the burrow of *Neürotrichus*.

Such a lateral stroke cannot be effected by extension of the forearm by contraction of the M. triceps, since the plane of the palm coincides with the plane of motion of the forearm. If, however, the humerus be held dorsally with the forearm half-flexed, the latter will project anteriorly and the palm will be turned laterally. Contraction of the humeral rotators will now swing the forearm and manus through a 90° arc in a horizontal plane and a lateral thrust has been achieved. Such a stroke is actually only the first half of the "breast-stroke" previously described, and this fact demonstrates the extremely limited pattern of a talpid's burrowing action.

Since the M. triceps cannot be used to thrust the palm against the soil, its great hypertrophy, accompanied by growth of the olecranon process in the more fossorial forms, must be explained in some other way. Freeman (1886) suggested that the long head of the M. triceps in *Talpa* would flex the humerus by drawing the olecranon toward the scapula; this may be correct for the talpines, although I cannot prove or disprove it. In *Neürotrichus*, however, the origin of the long head of the M. triceps does not extend posteriorly far enough upon the scapula for effective action as a flexor of the humerus.

If the long head of the M. triceps of the talpines does not act to retract the humerus, this system does not become a lever of the second class, as might be thought at first. Since the muscle is actually retracting the whole arm and not the humerus alone, the power is applied at the elbow, midway between the weight against the hand and the fulcrum at the shoulder-joint. The system forms, therefore, a lever of the third class.

The triceps complex and the opposing Mm. brachialis and pronator radii teres act as synergists in controlling the degree of flexion and extension of the forearm in the digging stroke. If the long head of the M. triceps, especially in the Talpinae, acts as a retractor of the whole arm, the hypertrophy of the Mm. brachialis and pronator radii teres can be explained, since a digging stroke is not always made with the antibrachium fully extended, yet contraction of the long head of the M. triceps will extend the forearm as well as retract the whole arm. Therefore the muscles opposing the long head of the triceps must be powerful if they are to maintain the antebrachium in a state of partial flexion.

Most of the force of any talpid digging stroke is transmitted to the manubrium through the clavicle and humerus. The humerus is held in position by the muscles acting upon it, by the double nature of the shoulder-joint, by the tendons of the muscles inserting across the shoulder-joint, and by the ligaments of the joint.

The talpid clavicle, however, has no such elaborate devices for maintaining its position; it projects anterolaterally and would, under lateral pressure from the humerus, be adducted anteromedially if it were not for the posterior pull of the Mm. costoscapularis ventralis and subclavius. These muscles, alone, hold the clavicle in place; the acromioclavicular ligament serves to hold the head of the scapula in place and is not a brace for the clavicle.

It is my opinion that talpid locomotion within the burrow is accomplished by use of the same pattern of extension and retraction of the fore limb as has been described in the burrowing stroke; the animal pulls itself forward instead of pulling earth backward. When upon the surface, the action of the fore limb is primarily the same, although here a talpid does not have the lateral walls of its burrow into which it can dig its claws; the animal must contact the substrate.

Desmanine moles easily accomplish such contact, inasmuch as the humerus projects laterally, the semi-flexed antebrachium projects anteriorly, and the manus automatically assumes a position flat upon the ground. The hand being fixed upon the ground, rotation of the humerus, which would draw the hand posteriorly in the digging stroke, pulls the shoulder-girdle, and consequently the body, forward. In desmanines the humerus is probably depressed for locomotion upon the surface and elevated for the burrowing stroke. In addition the M. trapezius anticus can elevate the whole shoulder-girdle; such action cannot be accomplished by talpine moles due to the shortness of the clavicle, and consequently the muscle has degenerated.

The humerus of a talpine mole projects dorsolaterally; thus the antebrachium must be completely flexed for the manus to reach the ground. With the fore limb in this position retraction of the humerus would lift the manus from the ground, but rotation of the humerus will twist the fore limb in an arc anteriorly around (not over) the point of contact between the manus and the substrate, and an awkward and difficult locomotion results. On the surface, a talpine attempts to assume the position normal for *Neürotrichus* when running, but the humerus is never depressed to the horizontal, and consequently the palm can never be placed flat upon the ground.

Talpid locomotion thus remains the same whether the animal is burrowing, running in the burrow, or progressing above ground. Rotation and retraction of the humerus furnish the basic power stroke; due to the 90° torsion (pseudosupination) of the ulna and radius the plane of the manus coincides with the plane of forearm movement so that extension and retraction of the antebrachium is useful only in the determination of the level at which the power stroke is to be applied.

TALPID EVOLUTION

The foregoing observations concerning talpid locomotion and shoulder construction are particularly interesting in view of the theory proposed by Campbell (1939) that the Talpidae became fossorial after a period of

aquatic adaptation. He based this conclusion upon the following points: (1) *Uropsilus* is a talpid so primitive that it is almost a shrew; its shoulder-girdle is wholly unsuited for burrowing; (2) any hypothetical fossorial but non-aquatic ancestor would have had clavicles longer than *Condylura* (or *Neürotrichus*, I might add) but shorter than *Uropsilus;* such an animal would be poorly fitted for either running or digging; (3) the peculiar locomotion of the mole, so aptly described as "swimming" has been derived from an aquatic ancestor which later adopted this same "breast-stroke" for burrowing in soft banks of streams; subsequent abandonment of the aquatic for the fossorial life further molded the shoulder-girdle but did not fundamentally alter the type of digging stroke; (4) the poorer burrowers among the talpids are still aquatic (*Desmana* and *Galemys*), semi-aquatic (*Condylura*), or tend to confine themselves to a wet environment (*Scaptonyx, Neürotrichus,* and *Urotrichus*).

I cannot see that Campbell's conclusions are necessarily correct, and will consider his evidence in some detail.

Campbell and I agree that the shoulder-girdle of *Uropsilus* represents a primitive intermediate stage in the evolution of the talpids from a soricid-like ancestor, and that this shoulder-girdle is not, itself, adapted for burrowing. We agree that the talpid shoulder-girdle, which is characterized by the humeroclavicular joint, did not arise as a fossorial adaptation. But Campbell's whole thesis is that the humeroclavicular joint did arise as an aquatic adaptation. If so *Uropsilus* should be aquatic to some degree. Dobson (1883) spoke of the animal as "terrestrial," and from what I can find in the literature it would seem that *Uropsilus* is not in any way aquatic.

I differ from Campbell in that I consider that the humeroclavicular joint could have first developed quite fortuitously, perhaps in answer to no environmental or locomotor need. Certainly this joint, in its primitive nature, could have been of little use to a purely terrestrial animal, neither does it necessarily hinder terrestrial locomotion.

Once some new anatomical structure has been achieved, such as a humeroclavicular joint, natural selection can mold that new character. In the Talpidae, the character allowed the animals to burrow in a way no other group could do. Evolution is not, of course, straight-line progress, and in the Talpidae divergent genera have developed their burrowing capabilities at different evolutionary rates, so that we can trace the series from the purely terrestrial form, as *Uropsilus,* through the partly terrestrial and partly fossorial form, as *Neürotrichus,* to the more fossorial talpines. Once the primary adaptation has been achieved, I see no necessity for an aquatic interlude.

At the time (upper Eocene?, lower Oligocene?) that the primitive talpids were in their most awkward intermediate stage of evolution, mammalian predators were not developed to such a degree of mental or physical efficiency as they are today, and this factor may have allowed a group of primitive talpids to maintain themselves during a critical evolutionary period. Avian predators were possibly more nearly developed to their present state of

efficiency than were mammalian predators, but avian predators may not have been an important factor in the survival of the small talpid-ancestor, which probably sought dense cover and may have been nocturnal.

Campbell overlooked, I think, one factor in the fossorial possibilities of a primitive talpid. In such an animal the clavicle is long and projects anterolaterally, it is true, but it articulates with the humerus and can bear the stress of lateral thrusts from the humerus if there is some mechanism present to keep the clavicle from swinging anteriomedially under the strain. In every talpid, except possibly *Uropsilus*, I am convinced that there is such a mechanism; that is, the Mm. costoscapularis ventralis and subclavius held the clavicle posteriorly and allowed the animal to be fossorial. For evidence concerning this point, *Uropsilus* must be dissected to discover the arrangements of these muscles in this nonfossorial, but potentially fossorial, talpid ancestor-type.

Campbell stressed the fact that a hypothetical semifossorial but non-aquatic ancestor would have had long clavicles, ill-adapted for terrestrial or fossorial life. This is true; *Neürotrichus* has remained in this stage and is confined to narrow ecologic and geographic ranges because it is neither a good runner nor burrower. But every group that has achieved some particular specialization has undoubtedly survived a poorly-adapted, intermediate stage in evolution (consider the bats, for instance). It is true that the fossil record includes many groups which have not survived such intermediate stages; this does not prove that such survival is impossible. Once the group is over the hump, so to speak, of the intermediate stage, the specialization can begin to pay dividends and geographic radiation will occur, although the group as a whole may be limited ecologically by the nature of the specialization. The talpines have been thus limited, but geographically have spread throughout the Palearctic region and can be classed as a successful group.

Campbell stressed *Galemys* as an intermediate aquatic type: "... in the stage represented by *Galemys* the clavicles are so long and set at such an angle (anterolaterally) that they can be of little use in the production of lateral force necessary in this curious method of digging and yet the forefeet are set in such a position as to place the animal at a great disadvantage on the surface of the ground. The aquatic environment is exactly suited for this type of animal. The fore limbs are placed at the sides where they possess a better mechanical advantage in swimming and yet are suitable for burrowing in the wet, soft soil of the banks. In short, an aquatic stage would provide a suitable solution to the necessary transition from the cursorial to this unusual fossorial environment."

Although I can find no description of swimming for either *Desmana* or *Galemys*, the great hypertrophy of the hind limbs as compared with the fore limbs, the webbing of the hind toes, and the large, laterally compressed tail of *Desmana* (the tail of *Galemys* is compressed only at its tip) strongly suggest that the fore limbs are not used extensively, if at all, in

swimming. If this assumption is true, the peculiar talpid shoulder-girdle and fore limb have been retained in the desmans chiefly for fossorial use and terrestrial locomotion. In other words I consider the desman to be a semi-fossorial animal which has secondarily become aquatic.

Gill ([1888]) stated the same conclusion; writing of the Desmaninae, he said: "These burrowing habits have been handed down by remote ancestors more fossorial than natatorial in habit."

Campbell discussed, but did not stress, the fact that those talpids which are less suited for a fossorial life are usually aquatic, semi-aquatic, or inhabit perpetually damp environments. It is only natural, in my oninion, that the genera which are not excellent diggers should be found in an environment where digging is easy. That they have, at the same time, become semi-aquatic (*Condylura*) or almost wholly aquatic (*Desmana* and *Galemys*) is not surprising. *Neürotrichus,* although not usually considered even semi-aquatic, is a superb swimmer in the wild (A. W. Moore, personal communication).

Indeed, all talpids that have ever been tested are excellent swimmers, but *Neürotrichus* and *Scapanus,* the only genera in which swimming has been adequately observed (Dalquest and Orcutt, 1942; and Reed and Riney, 1944, respectively) use the feet on each side of the body alternately when swimming. This motion is completely different from the aquatic "breast-stroke" supposed by Campbell to be ancestral to the talpid digging stroke.

The subject is not yet closed, however, as the swimming stroke of the more primitive talpids needs to be described. Even when an animal is observed, different investigators may not agree; thus Schmidt (1931) described *Condylura* as swimming with a breast-stroke and Lyon (1936: 36) described it as swimming with alternate strokes of both front and hind feet.

Summary

Divergent evolution within the superfamily Soricoidea (Mammalia: Insectivora) has produced, among other genera, the fossorial mole (*Scapanus*), the semi-fossorial, semi-cursorial shrew-mole (*Neürotrichus*), and the non-fossorial, semi-cursorial shrew (*Sorex*). Detailed dissections were made of the limbs of these three genera; the dimensions of each element of the appendicular skeleton and of the major parts of the axial skeleton were analyzed statistically with reference to the body length; and the muscles of the fore limb of *Scapanus* and of *Neürotrichus* were measured volumetrically. Correlation of these data with observed behavior of living animals has revealed the manner and degree of the locomotor adaptations in each genus.

Locomotion in *Sorex* is of a generalized type; the limbs are delicate, are held beneath the body, and move in a fore-and-aft plane. The appendicular skeleton is of an unspecialized monodelphian pattern and the feet are digitigrade.

All moles (Talpidae) are characterized by a shoulder-joint double in

nature, the usual joint being present as well as one between the greater tuberosity of the humerus and the clavicle. This bracing of the humerus by the clavicle allows the animal to burrow by thrusting laterally against the soil, whereas all other burrowing mammals loosen the soil by rapid anteroposterior strokes of the fore limbs. Even in a primitive mole (*Neürotrichus*), which has longer and more anteriorly directed clavicles than has a more specialized mole (*Scapanus*), the clavicle can support medial thrusts from the humerus because the posterior pull of the Mm. subclavius and costoscapularis ventralis holds the clavicle in position.

Important fossorial adaptations in the fore limbs of moles are as follows: the pectoral girdle has migrated anteriorly and the manubrium has lengthened accordingly; the manubrium has deepened ventrally; the clavicles have shortened and thickened; the scapula has become narrow and rodlike and the infraspinatus fossa is disappearing; the humerus projects laterally (*Neürotrichus*) or dorsolaterally (*Scapanus*) and has broadened; all processes of the humerus have increased in size, the tendon of origin of the M. biceps brachii is enclosed in a transverse tunnel in the proximal end of the humerus; pronation and supination are impossible due to the elbow and wrist being hinge-joints but the antebrachium has undergone a 90° supination due to torsion with the result that the plane of the manus coincides with the plane of forearm extension; a flexor check-ligament has developed between the humerus and the digits; and the manus has enlarged into a digging tool with long, stout claws. For all fossorial characters *Scapanus* is more specialized than is the primitive *Neürotrichus*. The latter has retained a long antebrachium for rapid running and can depress the humerus until the palm can be placed upon the ground; *Scapanus* can place only the medial edge of the manus upon the ground and is an awkward runner.

Rotation of the true medial side of the humerus posteriorly by the Mm. teres major, latissimus dorsi, subscapularis, and pectoralis superficialis posticus, all greatly hypertrophied, swings the forearm and hand posteriorly through an arc. This rotary movement of the humerus is the basic talpid locomotor action, both for digging and for running. The contraction of the powerful M. teres major would displace the vertebral end of the scapula lateroventrad were it not for the M. rhomboideus posticus, which runs across the back between the two scapulae; in *Scapanus* a part of this muscle has become tendinous.

In *Neürotrichus* the M. trapezius anticus elevates the skeleton of the shoulder-joint; in *Scapanus* this joint is more firmly fixed due to the shorter clavicle, and the muscle has degenerated.

In the hind limb the parts of the pelvic girdle of *Scapanus* are more firmly ankylosed, and the tibia, fibula, and pes are shorter and broader than in *Neürotrichus* or *Sorex*. These modifications of *Scapanus* are for more powerful action of the pelvic limb necessitated by the act of bracing while burrowing and the act of pushing accumulated dirt from the burrow.

The muscles of the hind limbs of the three genera are similar except that the M. peroneus digiti quarti is lacking in *Scapanus*.

Evidence is presented to show that the Talpidae did not necessarily develop from an aquatic ancestor, as suggested by Campbell (1939).

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Observations on the Breeding Habits of the Red-eyed Towhee

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A number of years ago the writer made a study of the breeding habits of the Red-eyed Towhee (*Pipilo erythrophthalmus erythrophthalmus* Linnaeus) in the vicinity of Morehead, Rowan County, Kentucky. Many species of fringillids have been studied, but there still appears to be little available information pertinent to the habits of this interesting sparrow.

Selection of territory.—Previous to the middle of March, the towhees remained together in definite flocks with a heavy preponderance of males. In the latter part of March these flocks began to break up, and as the weather became warmer the birds drifted farther and farther apart until each male had established a definite breeding territory. An influx of migratory birds occurred during late March and early April and supplied nearly every resident male with a mate.

After the nests were established, it was observed that on many occasions towhees drove blue jays and brown thrashers away from the vicinity of the nest, yet allowed Kentucky warblers and white-eyed vireos to feed within four or five feet of the nest without exhibiting the least concern.

Relation of territory to vegetation.—Jones (1889) reported "the bird is not partial to underbrush; but as often nests in the open woods among the leaves, or in neglected fields, or even in the corn-fields." Batchelder (1890) and Roberts (1932) reported towhees most common in second growth areas. In several instances observed by the writer, the territory consisted of two units, one primarily herbaceous, the other primarily woody. However, such was not always the case. In no instance might the plants have been called primarily herbaceous, but in several instances they were practically all woody.

Courtship.—Quite in accord with the courtship activities of other birds, the towhees observed employed three distinct methods of courtship, namely song, calls, and display. Song was by far the most widely used method of courtship. Before beginning to sing, the male towhee almost invariably went through a very characteristic performance. He flew to a small tree or shrub and began hopping about, always upward, calling almost continuously. As soon as the topmost branch was reached he threw back his head, drooped his tail, and began to sing.

Numerous writers have endeavored to apply syllables to the most common song of the towhee. Of these, that of Chapman (1934) "sweet bird s-i n-g," is perhaps the most appropriate.

Unusual and little known songs from the towhee are not at all uncom-

mon, having been noted by numerous writers, among them Saunders (1935), Dawson (1903), and Allen (1922). At numerous times the writer has observed towhees to utter unusual and often surprisingly beautiful songs.

Four distinct calls were used by towhees during the mating season. By far the most common of these was the familiar "tow-hee." The other calls noted were a simple "wee," a buzzing sound of three notes, and a rapidly repeated "chee-chee-chee-chee."

No doubt display plays an active part in the courtship of towhees, but only once was any behavior resembling display noted. In this instance the female took the active role. She perched on a twig a few feet in front of a male, fluffed her feathers, spread her wings and tail, and uttered the rapidly repeated "chee" noted above.

First nest.—The earliest nesting record the writer was able to find in the literature was that of Bailey (1913), who reported the towhee nesting in Virginia in the middle of April. The earliest nest observed by the writer contained one egg on April 4. Four other nests were known to be completed on April 18, 19, 25, and May 6.

Burleigh (1931) reported that the towhee "consistently avoids, during the summer months, thickets and underbrush in the open valleys and breeds only on the open mountain sides." The writer did not find this to be exactly the case. The exact location of six first nests was known, and of these, four were situated on the ground on the sides of hills, at distances varying from three to 50 feet from their base; one was situated on the ground in a brushy hollow about 75 yards from the base of a hill; the other was situated a few inches above the ground on a small stump which stood on the steeply sloping side of a brush grown bayou. Oberholser (1938) and Dawson (1903) have reported that the nests were occasionally roofed over, similarly to those of ovenbirds.

Each of the five nests that were situated on the ground was overhung by some type of vegetation. One was overhung by a bunch of dry grass, one by small huckleberry bushes, and three by sticks and dried leaves. In none of the nests observed was this overhanging vegetation placed above the nest. In each instance, the birds selected the site of the nest at the base of a clump of grass or upright projection of sticks and leaves. A cavity was scratched in the humus and the nest constructed in this cavity, leaving the vegetation overhanging the nest.

The nests examined by the writer were constructed largely of dead leaves, dead weed stems, pine needles, grasses, and strips of bark from grape vines. Grape vine bark seemed to be a favorite material, as a large percentage of four of the six nests examined was of this material. Each of the nests examined was lined with fine grasses and small weed stems. The lining was found to be very variable. In some nests it was complete, and in others only a small amount of material at the bottom of the nest. The outer portion of the nest consisted largely of dead leaves and grape bark.

In all nests observed by the writer, egg-laying was begun on the day the nest was completed or in the early morning of the succeeding day.

The number of eggs in a complete clutch has been variously reported from three to six, with four or five the most common number. Five nests were observed that contained four eggs each, and one was observed that contained only one egg. The latter nest also contained one cowbird egg. In this case, the towhee laid no more eggs, but incubated and hatched the two eggs.

The eggs of the towhee have been described by various writers, that of Reed (1904) being perhaps a typical one. He described the eggs as being "pinkish white, generally finely sprinkled but sometimes with bold markings of light reddish brown with great variations."

In the case of the first nests, incubation never was found to begin until the clutch was complete. Burns (1915) and Heil (1909), with whom the writer is in accord, have given the incubation period as twelve to thirteen days.

Heil (1909) and Forbush (1929) have reported that the male occasionally incubates the eggs to some extent. In the nests observed by the writer, incubation was performed solely by the female. In one instance the male

Fig. 1.—The second nest of a pair of Towhees. The presence of the bark of grape vines is an almost infallible characteristic of the nests of towhees.

was observed to feed an incubating female, but in no case was he observed to incubate the eggs.

During the incubation period, the female was found to spend from one to fifty-two minutes of each session off the nest, the average trip being of thirty minutes duration. The time spent on the nest at any one sitting was found to vary from twelve to eighty minutes, the average sitting being forty-eight minutes. Upon returning to the nest from a foraging expedition, the female was very often accompanied by the male. She usually approached the nest from the same direction, alighting on the ground about thirty feet from the nest, and hopping along the ground to the nest.

When flushed from the eggs, different females behaved very differently. As a general rule, when flushed from the eggs the female fluttered away over the ground, with her feathers fluffed out, wings and tail drooped, calling anxiously all the while. Often the feathers on the top of the head were erected. She usually continued in this manner until she was about thirty feet from the nest, at which point she generally forsook the ground for the trees.

Second nest.—Numerous writers are agreed that the towhee usually, or at least occasionally, rears two broods. Of the six pairs of birds building the first nests noted above, only two were known to build second nests. One of these pairs of birds had successfully reared a previous brood. In this case, the young of the first brood were forty-six days of age when the second nest was completed. The second nest was located two hundred and twenty-one feet from the first nest. The first nest of the other pair had been broken up fourteen days before the second nest was completely constructed. In this case the second nest was three hundred and fourteen feet from the first nest.

The second and third nests examined by the writer were located at varying distances from the ground. Numerous writers have reported towhee nests that were located off the ground. These nests range from a few inches off the ground to two located six feet from the ground, as reported by Porter (1908). The height of nine (presumably all second and third) nests located off the ground was found to vary from two feet six inches to nine feet four inches, the average being fifty-four inches.

As was the case in the first nests, incubation was begun the day the last egg was laid, or on the following day. In each of the two second nests, three eggs made up the entire clutch.

Third nests.—The second nest of one of the pairs of birds mentioned above was destroyed, and the birds again built a nest, this time one hundred and seventy-six feet from the second nest. Three eggs were deposited in the nest, which was destroyed a few days after the clutch was complete.

The young in the nest.—Eighteen stomachs from nestlings varying from one to eight days of age were examined; food items were (percent by volume): Lepidopterous larvae, 30.77%; Adult Coleoptera, 15%; Orthoptera, 10%; Lepidopterous cocoons, 7.22%; Coleopterous larvae, 6.68%; Arachnid

eggs, 3.61%; Adult Arachnida, 2.78%; Hemiptera, 0.83%; Dipterous pupae, 0.83%; Mollusca, 0.61%; Crustacea, 0.28%; inorganic matter, 21.39%.

For the first few days the food consisted of soft larvae, but as the birds grew older, harder foods and subsequently small stones were brought to them.

A total of fifty-three feedings were observed in 19 hours 23 minutes of observations; twenty-two were performed by the male. All the young in the nest were fed at each visit of a parent bird.

Very little brooding was observed except on the day the young hatched and on rainy days thereafter. The female alone was observed to brood the young, but on numerous occasions the male was observed to sit quietly on the edge of the nest for periods varying from a few seconds to fifteen minutes.

Figs. 2, 3.—2. Female Towhee brooding young. 3. Six-day-old Towhees in a nest located on the ground.

Both sexes were observed to remove excreta from the nest. In some instances the excreta was eaten, and in others it was carried several feet from the nest and dropped.

A few minutes after the young hatched, they were able to hold up their heads, move their legs and wings feebly, and grasp with their toes. At a few hours of age they were able to utter a faint "tsip" audible for several feet. At four days of age, the eyes opened, and the young were able to sit up on their abdomen and heels. At seven days of age the young were very restless and crawled about over the nest. The young that were weighed daily left the nest at this age.

Audubon (1856) reported that the young leave the nest "long before they are able to fly." Heil (1909) reported that "the young leave the nest when they are nine or ten days old."

In all the nests observed by the writer, the young, if disturbed to any great extent, left the nest at the age of seven days. In one nest the young were not molested until they were eight days old. When the writer came within six feet of the nest on this day, the three young clambered out of the nest, jumped three feet to the ground, and made off through the underbrush.

Enemies and parasites.—The fact that the towhee is victimized by the cowbird has been noted by many writers, among them Sanborn and Goelitz (1915), Roberts (1932), Dawson (1903), Poling (1890), and Friedmann (1938). Of the six first nests observed by the writer, two were parasitized by the cowbird. In one of the nests was one egg of the cowbird, and in the other, two.

Numerous animals have been reported as feeding on towhees, among them weasels (Audubon, 1856), the short-eared owl (Sage, Bishop, and Bliss, 1913), the sharp-skinned hawk (Sutton, 1928), and the bull snake (Nauman, 1929).

The eggs in one nest observed by the writer were devoured by a pilot black snake, *Elaphe o. obsoleta.*

Of the invertebrate enemies of the towhee, Peters (1936) has listed several species of lice, flies, ticks, and mites. During the course of this study, several specimens of a new species of *Dispharynx* were collected which were subsequently described by Olson (1939) as *Dispharynx pipilonis.*

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A Systematic Study of the Main Arteries in the Region of the Heart — Aves XXII

Passeriformes—Corvidae, Part I[1]

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Introduction

Garrod (1873) described the Passeriformes as "aves laevo-carotidinae" and assumed that the right carotids were absent, but as the present writer has demonstrated several times, the right vessels are reduced and become functionally modified during embryonic life. The left internal (trunk) carotid alone enters the hypapophysial canal to supply the head.

While there are many minor individual or even subfamily differences among some families of passerine birds, still other families appear to present a well-defined characteristic family arrangement-pattern. It has been assumed that where wide variations in the arterial pattern appears, within a family or order, that this is probably due in large part to divergence in evolution, while close similarity appears to indicate end-line or terminal evolution, with respect to this organ system.

Specimens of *Perisoreus c. canadensis* (Linnaeus), *Corvus b. brachyrhynchos* Brehm, *Cyanocitta c. cristata* (Linnaeus), and *Cyanopica cyanus interposita* Harlett were studied.

Corvus b. brachyrhynchos (Fig. 1): both the ligamentum aortae (5) and the ligamentum botalli (6) are present and maintain a proximal attachment with the pulmonary artery (7); the innominate (2) divides to form the common carotid (8) and subclavian (9) arteries; the subclavians give rise to the coracoid major (10), axillary (11), intercostal (12), and two pectoral (13) arteries in order; the right common carotid gives rise to the thyroid (21), superficial cervical (17), vertebral (14), ascending-oesophageal or right internal carotid (20) arteries, while the right syringo-tracheal artery (15) arises near the base of the ascending oesophageal artery; the left common carotid gives rise to a thyroid, vertebral, and left internal (trunk) carotid (19) arteries; the vertebral (14) sends off syringo-tracheal (15) and oesophageal (16) branches before giving rise to the left superficial cervical (17), while the scapular arteries (18) arise as branches of the superficial cervicals. The ductus shawi was not observed, but may be present arising from the common carotid arteries. The left internal carotid (19) alone enters the hypapophysial canal and passes anteriorly to the head.

1 Contributions of the Blue Sea Lake Biological Laboratory, Messines, P. Q.
2 Visiting Lecturer, College of Wooster, 1949-50.

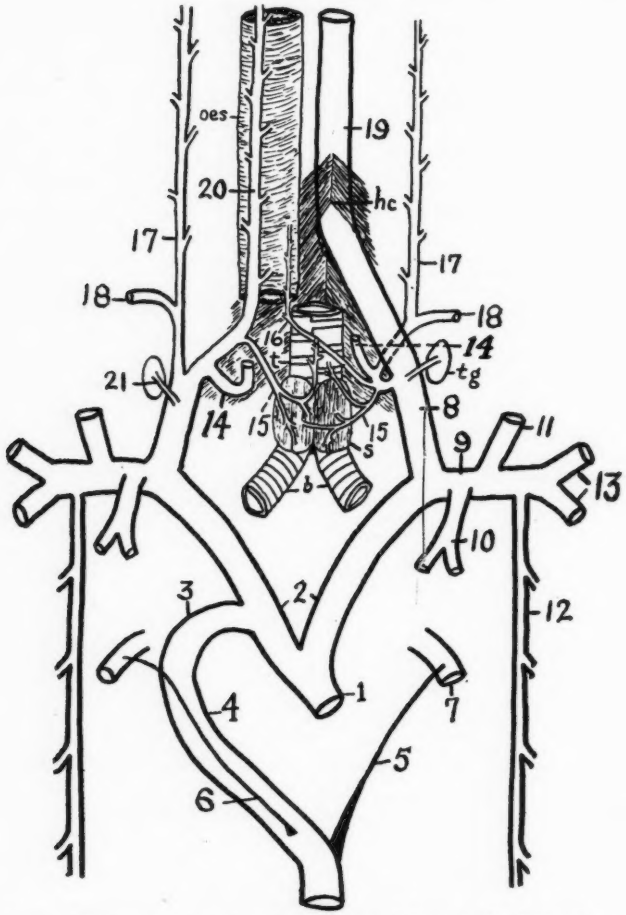


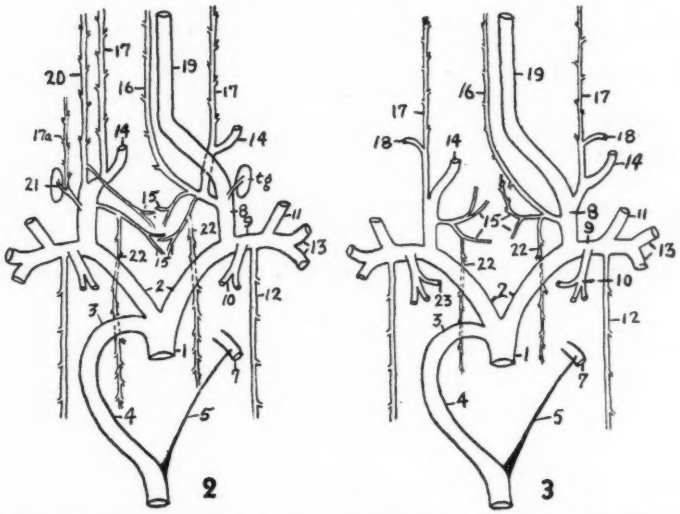
Fig. 1.—Diagram of arteries in neck and thorax of *Corvus b. brachyrhynchos.*

ABBREVIATIONS: 1. aortic root; 2. innominate arteries; 3. right systematic arch; 4. right radix aortae; 5. ligamentum aortae; 6. ligamentum botalli; 7. pulmonary artery; 8. common carotid artery; 9. subclavian artery; 10. coracoid artery; 11. axillary artery; 12. intercostal artery; 13. pectoral arteries; 14. vertebral artery; 15. syringo-tracheal artery; 16. secondary oesophageal artery; 17. superficial cervical artery; 17a. accessory cervical artery; 18. scapular artery; 19. left internal carotid (trunk) artery; 20. ascending-oesophageal (right internal carotid) artery; 21. thyroid artery; 22. ductus shawi; 23. sterno-tracheal artery; b. bronchi; hc. hypapophysial canal; oes. oesophagus; s. syrinx; t. trachea; tg. thyroid gland.

Cyanocitta c. cristata: as is *Corvus*, both the ligamentum aortae and the ligamentum botalli are present. The branches of the subclavian arteries are the same as in *Cyanopica* below. The branches of the common carotid are as in *Corvus* above.

Cyanopica cyanus interposita (Fig. 2): the ligamentum aortae (5) is present, but the ligamentum botalli is lacking; the subclavians give rise to the coracoid major (10), intercostal (12), axillary (11), and two pectoral (13) arteries in order; the right common carotid gives rise to the ductus shawi (22), and this in turn gives off the syringotracheal artery (15), the accessory superficial cervical (17a), from which is derived the thyroid artery (21), the ascending-oesophageal (20), superficial cervical (17) and the vertebral (14) arteries; the left common carotid gives rise to the thyroid artery (21), vertebral, and left internal carotid (trunk) (19) arteries; the left vertebral artery sends off the ductus shawi (22) and the oesophageal artery (16) before giving rise to the superficial cervical artery (17). A syringo-tracheal artery (15) arises from both the left oesophageal artery (16) and the ascending-oesophageal artery (20).

Perisoreus c. canadensis (Fig. 3): the ligamentum aortae (5) is present and prominent, while as in *Cyanopica* the ligamentum botalli is completely atrophied; the subclavian gives rise to the coracoid major (10), axillary



Figs. 2, 3.—2. Diagram of arteries in neck and thorax of *Cyanopica cyanus interposita*; 3. Diagram of arteries in neck and thorax of *Perisoreus c. canadensis*. (See fig. 1 for key to abbreviations.)

(11), intercostal (12), and two pectoral (13) arteries; the sterno-tracheal (23) arises as a branch of the coracoid major; the right common carotid gives rise to the thyroid artery, ductus shawi (22), with its branches to the trachea and syrinx, the superficial cervical (17), and vertebral (14) arteries; the left common carotid gives off a thyroid artery, ductus shawi, vertebral, and left internal (trunk) carotid (19) arteries, while the left vertebral gives rise to the left superficial cervical (17), and the oesophageal artery of this side (16) arises as a branch of the left ductus shawi. Scapular arteries (18) arise as branches from the superficial cervical arteries. No ascending-oesophageal artery was observed on the right side, but the right superficial cervical artery was found to deliver several branches to the oesophagus.

It may be seen from the above observations that no two species presented identical arrangement-patterns, but that there are certain fundamental similarities in all of the forms.

These differences may indicate progressive divergence in the developmental evolution among members of this family, and as a result, it may be concluded that the Corvidae do not represent a well-defined terminal group of birds. If this is true, further studies on other species of this family may tend to show lines of divergence, although the basic pattern may not be expected to vary greatly from the more generalized family arrangement.

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Distribution of the Carabidae (Coleoptera) of Boulder County, Colorado*

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Introduction and Acknowledgment

The effect of altitude on the distribution of insects has not been widely studied, and except for isolated observations, no work has been done on the vertical distribution of the ground beetles (Carabidae). It is the purpose of this thesis to show the distribution of the Carabidae throughout the altitudinal zones of Boulder County, Colorado.

The Carabidae is a large and important family of Coleoptera and is world-wide in its distribution. The species are predatory and many are definitely beneficial since they attack other insects which are plant pests. Because of this carnivorous habit, the carabids are dependent only indirectly upon vegetation for their existence.

An interest in this group of insects was developed by the writer during a field course in entomology in the summer of 1946, and some collections were made at that time. Most of the collecting, however, was carried on between October 1946 and October 1947. In addition, there are in the writer's collection a number of specimens taken by R. E. and E. V. Gregg in 1944 and 1945, for which I am grateful.

Acknowledgement

I wish to express deep appreciation to Dr. William C. Stehr, Professor of Entomology at Ohio University, Athens, Ohio, for his invaluable assistance in identifying the species of Carabidae collected for this study. Dr. Robert E. Gregg and Dr. Gordon Alexander have given most helpful suggestions, criticisms, and supervision; and Dr. Hugo G. Rodeck, director of the University of Colorado Museum, has kindly given permission to use the Museum collection and records. I am indebted to the Misses Emma Davis, Ella Haubold, and Ida Malleis for assistance in collecting specimens and for providing transportation to the collecting areas.

History

The distribution of plant and animal life over the surface of the earth has been a matter of interest and investigation for many years. Since the time of Alexander von Humboldt, or before, it has been recognized that organisms are not universally distributed (Merriam, 1894). Wallace (1876), in his *Geographical Distribution of Animals*, gives us a classic interpretation which is probably the earliest comprehensive treatment of the subject. Previous to this, many other writers have observed and recorded the distribution of certain groups of plants or animals over the earth or limited areas thereof.

* The author's thesis for the master's degree at the University of Colorado, Boulder, 1948.

In North America, Latreille, Leconte, Scudder, and Schwarz have suggested major zones or regions upon the basis of their study of insects (Merriam, 1892). Their divisions are few and not well defined. Merriam, however, has established life zones which are much more clearly marked and distinct. These zones are the Tropical, Lower Sonoran, Upper Sonoran, Transition, Canadian, Hudsonian, and Arctic-Alpine. They are founded upon his observations of the latitudinal distribution of North American mammals, etc., and have temperature differences as their primary basis; and because temperature decreases with increasing altitude as well as with increasing latitude, we find a corresponding altitudinal distribution.

There are those, however, whose work seems to indicate an absence of zonation for some insect groups, at least in certain areas. Folsom and Wardle (1934) maintain that the insects do not conform with established life zones since they are "independent of minor climatic differences to a high degree." According to these authors, many North American insects are associated with the life zones of Ward which are based on rainfall types. Many species are limited to those areas within one rainfall type only.

Chopard (1945) found that the orthopteroid fauna between 1800 and 3000 meters on mountains in the Cameroon differs little from that of adjacent lowlands, and Leng (1912), in discussing the Cicindelidae, reports that "to attempt to define zones or regions for such a group is a hopeless task for scarcely any barrier is effective for all the species, all the time . . ."

Most of the evidence, however, shows that there exists a vertical zonation among some groups of insects, and that altitude affects insects in rather definite ways may be taken as an indication that zonation might be expected.

When or where zonation does exist among the insects, it is probably not altitude *per se* which is responsible. To substantiate this we have Darlington's (1943) statement that the lowland forms in Colorado live from 3500 to 4000 feet higher than the same species in the lowland habitats of New Hampshire.

Dodds and Hisaw (1925) attribute the zonation of aquatic insects to temperature differences, and Williams (1946) shows the correlation between temperature and rainfall and insect abundance; he also states that microclimates, or the immediate environment, affect their presence and their abundance.

Hesse, Allee, and Schmidt (1937) discuss the effects of altitude on insects generally. They contend that cold and lack of food rather than reduced pressure affect the distribution of cold-blooded animals. Alpine insects show either a shortened life history to accommodate a short summer or a much lengthened life span by reason of a reduced developmental rate in order that the insect may have two periods of growth and activity. The latter instance may be found among those insect orders having complete metamorphosis because the pupal stage would be able to survive the extreme winter conditions.

The alpine Coleoptera, according to the same authorities, are character-

istically small and wingless or flightless and are to be found in the most concealed places. Of 4000 species of beetles which were found in the Tirol, 272 were typically alpine and were often wingless.

Another instance of the effect of altitude on insects is to be found in the studies of Darlington (1943) on the relationship of wing atrophy to the distribution of mountain and island Carabidae. Those species found at high altitudes, especially where they are exposed, show a much higher percentage of wingless species or of species with their wings atrophied. In his analysis of the Carabidae from the Presidential Range in New Hampshire, Darlington indicates that the forest species are not distinctly isolated from the neighboring lowland forms but that there are arctic relicts which make up a true Arctic-Alpine fauna.

The ecology and life zones of the Presidential Range have been studied rather extensively from an entomological standpoint. Alexander (1940) lists the species of insects which are evidently alpine forms. The beetles of the Range are emphasized because they are better known than any other order due to the collections of Bowditch, Mrs. Slosson, Sherman, and others.

Van Dyke (1919a) states that the insect faunas of the Pacific Coast show a distinct zonation. He emphasizes distribution of Carabidae and says that characteristic species of the Hudsonian zone are very distinct, but that those of the Canadian zone are much less so.

Species of longicorn beetles in Argentina correlate with the life zones there, but in this case it is no doubt due to their feeding on specific plants. The monophagous forms were more limited in distribution than those which fed on a variety of plants (Bosq, 1943).

To test the validity of life zones in New Mexico, Cockerell used wild bees (Scudder and Cockerell, 1902). Of 414 species collected, only 153 were found in two or more zones. The remaining ones were restricted to one zone, and zonal boundaries conformed to those established for plants and other animal groups. The number of species in each zone decreased as the altitude increased.

W. M. Wheeler (1914), in his study of the ants of Hidalgo, Mexico, discusses the characteristics of high altitude forms, and from this one would infer that vertical zonation exists among the fauna of that region.

In a later study on ants, Wheeler compares the distribution of Transition and Boreal forms in four mountain areas of North America. Factors influencing zonation of the ant-faunas are slope exposure and a combination of warmth and humidity. He states that the results of this study "agree in the main with those derived from other animals and of plants . . ." (Wheeler, 1917).

In 1944, Wheeler and Wheeler found that, although most ant species are state-wide in North Dakota, there is some correlation with the life zones of that region. In Colorado the species of ants may be divided into at least three groups representing the plains, coniferous forest, and alpine zone, and possibly a fourth, or transition group (Gregg, 1947).

In the analysis of his collection of Rocky Mountain Coleoptera, Leconte (1878) lists those which he says "appear to be" strictly mountain forms. He also says that "it will be very interesting . . . to group the species according to the elevation by which they are limited." To date there seems to have been no organized attempt to do this for the Coleoptera of the Rocky Mountain region, although there are numerous records of species found at definite altitudes in scattered areas.

Throughout the life zones of Colorado, which include all except Tropical and Lower Sonoran, the altitudinal distribution of mammals has been established principally by Merritt Cary (1911) in a study for the Bureau of Biological Survey. He uses five of the life zones of Merriam; namely, Upper Sonoran, Transition, Canadian, Hudsonian, and Arctic-Alpine. Ramaley (1907) employs different terms which are, for all practical purposes, synonymous with the zone names of Merriam. These are plains, foothills, montane, sub-alpine, and alpine, respectively.

In the Colorado Rockies, Dodds and Hisaw (1925) have investigated the distribution of mayflies, caddisflies, and stoneflies. They report that these insects show an altitudinal distribution which bears a definite relationship to the life zones as recognized by Ramaley (1927) for plants of the region.

Among Colorado Acrididae there is a direct correlation between their vertical distribution and their seasonal appearance, although actual zonation is not discussed (Alexander, 1933).

With regard to the distribution of birds in Boulder County, Alexander (1937) states that it is difficult to recognize more than two zones between the plains and the alpine tundra. There is, however, a definite vertical zonation.

G. S. Dodds (1919, 1920) has made an extensive study of the Entomostraca in the Rocky Mountains of Colorado. His work shows only three distinct zones represented by characteristic species. These zones are plains, montane, and alpine.

The lakes at various altitudes in northern Colorado have been studied by Pennak (1941). According to him there are four limnological zones, the plains, foothills, montane, and alpine. In a later paper (Pennak, 1945) there is a discussion and comparison of the chemical and physical characteristics of these lakes.

An account of the geology, geography, and climate of northern Colorado, including Boulder County, may be found in Pennak's paper (1941), and detailed accounts of the zoology and botany of Colorado are given by Cockerell (1927) and Ramaley (1927). Accordingly, only a very brief summary of the life zones in Boulder County will be given here. The zone names used are those of Ramaley.

The plains zone which occupies the eastern third of the County up to the 6000 foot contour is characteristically grassland. The only trees to be found are cottonwoods and willows along water courses. Habitats include

grassland, wooded areas along creek banks, cattail swamps, roadside and railway right-of-way bordering cultivated fields, and vacant lots and gardens within city limits.

The foothills are distinguished by open forests of Ponderosa pine (*Pinus ponderosa*). Douglas fir (*Pseudotsuga taxifolia*) often grows on the north-facing slopes and the creeks in the canyon bottoms are lined with willow, alder, and cottonwood, and several types of shrubs such as sumac, choke-cherry, and mountain mahogany. This zone extends from approximately the 6000 foot level to 8000 feet. The north and south slopes and the canyon bottom provide a variety of environments.

A denser forest of Douglas fir and Lodgepole pine (*Pinus contorta*), with scattered groups of aspens (*Populus tremuloides*), is characteristic of the montane zone which extends from 8000 to 10,000 feet. In the canyon bottoms of the lower levels, however, there are Colorado blue spruce (*Picea pungens*) and Ponderosa pine.

Engelmann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*) constitute the climax forest of the subalpine zone with limber pine (*Pinus flexilis*) found in some areas. Near the upper edge of the subalpine zone, at about 11,500 feet, the trees are dwarfed and twisted and are termed "wind timber." The forest floor, open park-like areas, and the edges of streams in the mountain valleys are representative collecting areas in this and the preceding zone.

Above timberline is the alpine zone which is exposed, rocky grassland or tundra with dense thickets of dwarf willows in the more protected spots. Rocks provide places of concealment for beetles, whereas others may be along the edges of snow banks.

PROCEDURE

Boulder County is located in the north-central part of Colorado. It measures approximately twenty-five by thirty-five miles and lies immediately west of the 105th meridian. The fortieth parallel of north latitude crosses the southern part of the County.

Topographically, the land slopes from an altitude varying from 12,000 to 14,000 feet along the Continental Divide which marks the western boundary of the County, to 5000 feet in the plains area to the east. This is a drop of from 7000 to 9000 feet within a distance of thirty-five miles and results in sudden changes of weather and great climatic differences.

As many different types of environment as possible in each zone were selected as areas for collecting. Twenty-three collecting stations are indicated on a map (fig. 1). The identification of each station and a description of the habitat follows.

Station 1.—An area near Lyons, called Meadow Park, is on the very edge of the foothills. It is a wooded park bordering South St. Vrain Creek. Vegetation is like that of the foothill canyon bottoms so that it is distinctly a foothills station although at an altitude less than 6000 feet.

Station 2.—A roadside lined with grass and weeds southeast of Hygiene provided numerous rocks under which the carabids could find shelter.

Stations 3 and 4.—Along roadside and railroad right-of-way bordering cultivated fields close to Longmont, rocks, paper, tin cans, and other debris furnished places of concealment. Drainage ditches along the sides were without water, but where they were decidedly moist the number of species increased noticeably.

Station 5.—A creek bank just southwest of Longmont, bordered by a small, open grove of cottonwood and willow trees, provided a variety of ecological niches. The soil was thin, rocky, and sparsely covered with weeds and only a little grass. In one place there was a strip of fine, wet sand bordering the stream and at another point the stream had changed its course slightly and had left a gravel bed which was strewn with debris from high water.

Station 6.—This station is represented by vacant lots, lawn, and garden areas within the city limits of Longmont.

Station 7.—Several species were found near Canfield along a roadside similar to areas 2, 3, and 4, but considerably drier.

Station 8.—This high, rolling, arid region known as Fourmile Mesa is intersected by ditches formed by erosion. Vegetation is grass interspersed with cacti, thistles, yucca, and other dry-land plants.

Station 9.—Along a creek lined with cottonwoods and willows, a large number of beetles were found under old logs and bits of bark and in decaying wood. A sand pit in the same area was rimmed with debris deposited when the water had been over the edge of the pit.

Station 10.—A number of species, some of which were abundantly represented, were found on the University of Colorado campus in Boulder.

Station 11.—This is a cattail swamp along the roadside and adjacent to an irrigation ditch in a low area of the plains near Baseline Reservoir. Beetles were numerous beneath old and broken cattails which had fallen into the mud at the edge of the swamp.

Station 12.—Gregory Canyon is in the foothills near Boulder. An intermittent stream at the bottom flows in a generally northeast direction. The south wall of the canyon is covered with Ponderosa pine and a small amount of Douglas fir. Only a few scattered trees are on the north wall, but in the canyon bottom there is a dense growth of cottonwoods, willows, chokecherry, plum, wild grape, and sumac.

Station 13.—The south slope of Flagstaff Mountain forms a part of the north wall of Gregory Canyon. The peak reaches an altitude of 7000 feet. Species found here were on the road to the summit.

Station 14, 15.—These two collecting areas in Boulder Canyon have very similar foothills canyon bottom vegetation with the creek bank lined with willow, alder, and cottonwood trees.

Station 16.—About eight miles north of Boulder, Lefthand Creek issues from the canyon of the same name. The canyon is much like Boulder Canyon. Collections were made along the stream on the canyon floor.

Station 17.—Science Lodge, the University of Colorado Science Camp near Ward, is in the open coniferous forest of the montane zone. It is on a generally south-facing slope at an altitude of 9500 feet.

Station 18.—The region at Allenspark where collecting was done is an open, almost park-like area sloping gently and irregularly southeastward. Trees, in scattered clumps, are almost wholly lodgepole pine. The altitude varies from 8500 to approximately 9000 feet.

Station 19.—Just west of Allenspark, in the southeast corner of Rocky Mountain National Park, is Wild Basin. This mountain valley extends up into the subalpine zone. Collections were made along the trail from the ranger station to a point called Ouzel Falls which is two or three miles up the stream.

Station 20.—This is another mountain valley in the spruce-fir forest of the subalpine zone. West of Ward, it extends upward beyond Brainard Lake to Lake Isabelle. The altitude at Brainard Lake is 10,325 feet and at Lake Isabelle it is 10,850 feet.

Station 21.—Rocks near the foot of Arapahoe glacier afforded a number of beetles of apparently the same species. The rocks, at an altitude of about 12,500 feet, were completely surrounded by ice and snow in midsummer.

Station 22.—Carabids were collected just above timber-line on the north slope of Longs Peak. Tundra grasses, low-growing flowering plants, and dense masses of dwarf willows are characteristic.

Station 23.—This particular mountain, bearing the frequently encountered name, Bald Mountain, is a ridge extending eastward from the Arapahoe peaks. Both spruce-fir forest and alpine tundra are represented at this collecting station.

Carabidae for this study were collected from various habitats at each of the twenty-three stations (fig. 1). Most of the specimens were secured by overturning rocks and by searching debris which might afford shelter to the insects. At two stations, bait traps were used. Those traps made from raw potatoes, in which a hole had been bored almost through their length, did not yield any Carabidae. Other traps were constructed of large (number 10) tin cans. A small amount of a mixture of one part molasses and twenty parts water was placed in each container (Frost and Dietrich, 1929;

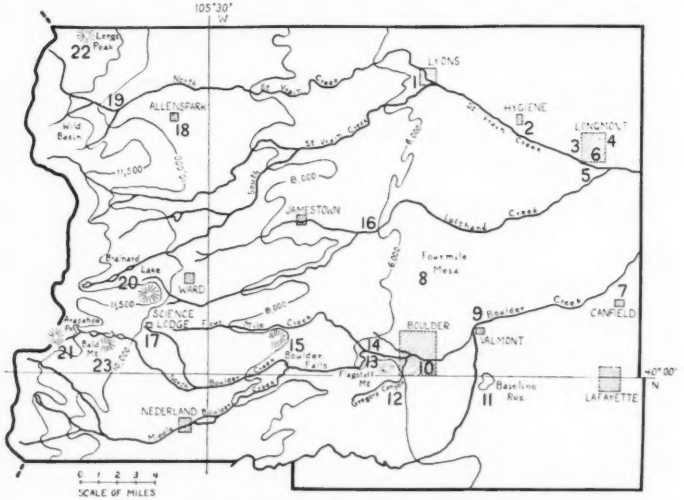

Fig. 1.—Location of collecting stations.

Peterson, 1934). These traps were sunk into the ground until the rim was level with the surface. Shingles, placed over them as protection from rain, were slightly raised by sticks or broken rock so that insects might approach the traps readily. Several species of Carabidae were attracted to these traps.

All specimens were mounted on standard entomological pins, the smaller ones first being glued to paper points (Banks, 1909). In addition to the customary data (location, date, and collector's name) on the pinned insects, each individual was given a serial number representing the exact locale from which it was taken. The serial numbers, with habitat notes, were kept in duplicate and all records were double-checked against each other and with the collection to eliminate any possibility of error in recording.

Determination of the genus for the larger specimens was made by the author after consulting the keys of Bradley (1930), Blatchley (1910), Essig (1926), and Sloane (1923); but the species and most of the genera were identified through the generosity of Dr. William C. Stehr.

The collection is comprised of 627 individuals representing 41 genera and 100 species. Thirty-three duplicates representing 11 genera and 15 species were retained by Dr. Stehr.

OBSERVATIONS

Most of the published material on the distribution of Carabidae is concerned with their origin or with those forms found at high altitudes. Especially important in this connection insofar as the continent of North America is involved are the studies of Blake (1945), Cockerell (1909), Darlington (1943), Fall and Cockerell (1907), Leconte (1878, 1879), Notman (1918), Sherman (1910), Snow (1904), Tanner and Hayward (1934), and Van Dyke (1919a, 1939).

Genera which contains species peculiarly adapted to high altitudes are *Amara, Bembidion, Carabus, Cryobius, Cymindis, Harpalus, Nebria, Platynus,* and *Pterostichus.* In no instance is the entire genus, however, restricted to the upper life zones, for there are species in each genus which are lowland forms.

Species of *Nebria* (Hesse, Allee, and Schmidt, 1937), *Bembidion* and *Platynus* (Van Dyke, 1919b) may be found in large numbers along the snow fields of the alpine zone in North America; and on the Mount Everest expedition, Andrewes (1930, 1934) found that the Carabidae were the predominant insects at high altitudes with species of *Amara, Bembidion,* and *Cymindis* at extremely high elevations.

In the Medicine Bow Mountains in Wyoming, species of *Celia, Harpalus, Carabus,* and *Pterostichus* have been collected from the alpine grasslands (Blake, 1945).

Carabus taedatus is the only carabid listed from above timber-line in Melander's (1921) collection of insects on Mt. Rainier; and Linsley and Michener (1943) report only one species, *Pterostichus ater* Leconte, in the Mt. Lassen vicinity during their studies of Coleoptera at that place.

Those species collected for this study in only the alpine and subalpine zones are *Bembidion incertum* (Mots.) and *Nebria purpurata* Leconte in Boulder County, and *Cymindis acomana* Casey and *Curtonotus brunnipennis* DeJean on Fall River Pass in Rocky Mountain National Park adjacent to Boulder County.

Other species found only at high altitudes were *Calathus coloradensis* Casey, *Carabus taedatus oregonensis* Casey, *Pterostichus lecontellus* Csiki, and *Cymindis unicolor* Kirby. The distribution of the six Boulder County species is shown in figure 2.

Nebria obtusa Leconte, which is usually listed as a species characteristic of high altitudes, was collected in the alpine zone; but one specimen was found along a creek near Valmont in the plains zone. The Bowditch collection contains specimens taken along the South Platte River in the foothills zone (Leconte, 1878). Whether the species has a greater range than was supposed or whether these individuals from the plains and foothills are accidentals is difficult to say.

It is probable that euryzonal and stenozonal forms occur according to the extent of their specific ecological requirements. Those forms which must occupy only one ecological niche in order to survive would have a much more limited spacial distribution than those which are able to adapt themselves to a variety of habitats.

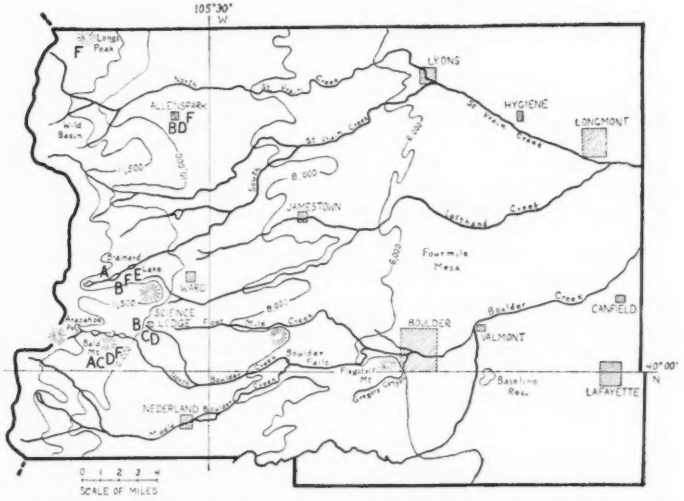

Fig. 2.—Species collected only in high altitudes. *Bembidion incertum* (A); *Calathus coloradensis* (B); *Carabus taedatus oregonensis* (C); *Cymindis unicolor* (D); *Nebria purpurata* (E); *Pterostichus lecontellus* (F).

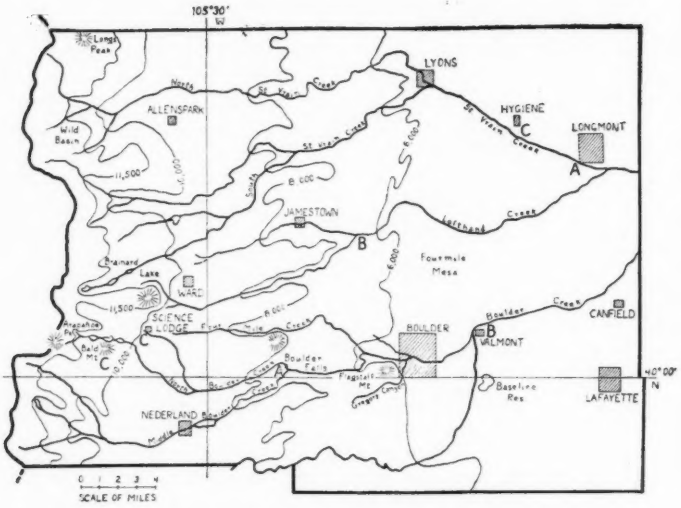

Fig. 3.—Species whose distribution is limited by moisture. *Bembidion lucidum* (A); *Harpalus compar* (B); *Triplectrus rusticus* (C).

That certain species occupy more than one zone may result also from the presence of similar habitats in each. Factors such as moisture, soil temperature, air temperature, evaporation rate, light, ground slope, vegetation, soil type, and soil texture influence the insect population of an area enormously. A few outstanding examples were observed and should the microclimates of each station be studied in detail, it is very probable that other instances would confirm the above supposition.

Bembidion lucidum (Leconte) and *Harpalus compar* Lec. were present along creek banks in the plains and foothills both. Their distribution is evidently limited primarily by amount of moisture. Another widely eurycolonal form from plains, montane, and alpine zones is *Triplectrus rusticus* (Say). It was under stones in rather moist places at each collecting station where it was found (fig. 3).

Five species of *Chlaenius*, collected only in the plains zone, were under broken reeds in the mud of the cattail swamp or in similar places such as along creeks and drainage ditches (fig. 4).

Table 1 is a list of all Carabidae collected, and following it, table 2 is a summary of species found in each zone or combination of zones. An annotated list, beginning on page 700, gives the stations and types of habitat where each species was found and additional records which have come to the attention of the writer.

TABLE 1.—Carabidae collected in Boulder County, Colorado

Species	No. of Specimens	Zones				
		P	F	M	S	A
1. *Agonoderus comma* (Fabr.)	9	×				
2. *A. obliqulus* Casey	3	×				
3. *Amara cupreolata* Putzeys	6	×				
4. *A. fallax* Leconte	8	×				
5. *A. impuncticollis* Say	1	×				
6. *A. lecontei* Csiki [= *polita* Leconte]	4	×		×		
7. *Anisodactylus harrisi* Lec.	2	×				
8. *Apristus subsulcatus* (Dej.)	1	×				
9. *Bembidion bifossulatum* (Lec.)	2	×				
10. *B. consanguineum* Hayward	2		×			
11. *B. coxendix* Say	1	×				
12. *B. dubitans* (Leconte)	1	×				
13. *B. incertum* (Motschulsky)	11				×	×
14. *B. lucidum* (Leconte)	2	×	×			
15. *B. nitidum* (Kirby)	1	×				
16. *B. patruele* Dejean	2	×				
17. *B. scopulinum* (Kirby)	6		×			
18. *B. stabile* (Leconte)	1		×			
19. *B. timidum* (Leconte)	1	×				
20. *Bothriopterus laxicollis* Csy.	2			×		
21. *B. saxatilis* Casey	8	×	×	×		
22. *Brachinus ballistarius* Lec.	1	×				
23. *B. cordicollis* Dej.	12	×				
24. *B. cyanipennis* Say	4	×				
25. *B. medius* Harris	1	×				
26. *B. minutus* Harris	1	×				
27. *Bradytus latior* Kirby	7		×	×		
28. *Calathus coloradensis* Casey	6			×	×	
29. *Calosoma calidum* Fabr.	1	×				
30. *Carabus serratus tatumi* Mots.	1		×			
31. *C. taedatus oregonensis* Casey [form *montanicus*]	4			×		×
32. *C. t. patulicollis* Casey	8			×		
33. *Celia ellipsis* Casey	4	×		×		
34. *C. farcta* Leconte	5	×				
35. *C. museulus* (Say)	4			×		
36. *C. scolopax* Casey	21			×		
37. *C. thoracica* Casey	2			×		
38. *Chlaenius diffinis* Chaudoir	9	×				
39. *C. impunctifrons* Say	14	×				

TABLE 1.—(*continued*)

Species	No. of Specimens	Zones				
		P	F	M	S	A
40. *C. pennsylvanicus* Say	16	×				
41. *C. sericeus* Forst.	16	×				
42. *C. tomentosus* (Say)	1		×			
43. *C. tricolor* Dejean	4	×				
44. *Cratacanthus dubius* (Beauvois)	9	×				
45. *Cryobius hudsonicus* Leconte	1			×		
46. *C. mandibularis* (Kirby)	1			×		
47. *C. riparius* (Dejean)	1			×		
48. *Curtonotus carinatus* (Lec.)	1	×				
49. *C. laticollis* (Leconte)	3	×				
50. *Cymindis unicolor* Kirby	7			×		×
51. *Eumolops sexualis* Casey	98	×	×			
52. *Harpalus amputans* Say	8	×				
53. *H. caliginosus* (Fabr.)	11	×	×			
54. *H. cautus* Dejean	1			×		
55. *H. compar* Leconte	12	×	×			
56. *H. curticornis* Casey	1		×			
57. *H. erraticus* Say	1	×				
58. *H. furtivus* Leconte	1			×		
59. *H. herbivagus* Say	11	×				
60. *H. lustrans* Casey	1			×		
61. *H. pennsylvanicus* DeGeer	3	×				
62. *H. pleuriticus* Kirby	2	×				
63. *H. probatus* Casey	1	×				
64. *H. seclusus* Casey	14		×		×	×
65. *H. sejunctus* Casey	6	×				
66. *Loricera pilicornis* Fabr. [= *caerulescens* L.]	3	×				
67. *Melanius* [= *Omaseus*] *caudicalis* Say	1	×				
68. *M. corvinus* Dejean	1	×				
69. *M. luctuosus* (Dejean)	2	×				
70. *Metabletus americanus* (Dej.)	5	×		×		
71. *Nebria obtusa* Leconte	4	×				×
72. *N. purpurata* Leconte	2				×	
73. *Nothopus zabroides* Leconte	1		×			
74. *Omaseulus* [= *Micromaseus*] *desidiosus* (Leconte)	2	×				
75. *Pasimachus elongatus* Leconte	6	×	×			
76. *Patrobus longicornis* (Say)	2		×			
77. *Percosia diffinis* Leconte	4	×				
78. *Philophuga amoena* (Leconte)	1			×		
79. *Platynus affinis* (Kirby)	1			×		

TABLE 1.—(*continued*)

Species	No. of Specimens	Zones				
		P	F	M	S	A
80. *P. decorus* (Say)	1	×				
81. *P. extensicollis* (Say)	24	×				
82. *P. melanarius* (Dejean)	23	×				
83. *P. placidus* (Say)	13	×				
84. *P. seminitidus* Kirby	4			×		
85. *Poecilus lucublandus* Say	13	×				
86. *Pristodactyla advena* (Leconte)	19			×		
87. *Pterostichus lecontellus* Csiki [= *longulus* Leconte]	26			×	×	×
88. *P. protractus* Leconte	11			×		
89. *Rembus obtusa* Leconte	1	×				
90. *Scaphinotus elevatus coloradensis* Van Dyke	1		×			
91. *Selenophorus* [*Selenophorus*] *pedicularius* Dejean	2	×				×
92. *S.* [*S.*] *planipennis* Leconte	4		×			
93. *Stenocellus rupestris* (Say)	3	×				
94. *S. tantillus* (Dejean)	3			×		
95. *Stenolophus conjunctus* (Say)	2	×				
96. *S. fuliginosus* Dejean	1	×				
97. *Tachyura dolosa* (Leconte)	11	×				
98. *T. incurva* (Say)	16	×				
99. *Triplectrus rusticus* (Say)	3	×		×		×
100. *Trechus chalybeus saxatilis* Casey	1			×		
Total	627					

That there are so few species recorded from the subalpine zone is no doubt due in part to the shorter time spent in collecting at those stations. In addition, it is a recognized fact that as altitude increases, the number of species as well as the number of individuals decreases; and for the Carabidae, a lack of variety of habitats probably is an important contributing factor.

Any species represented in the collection by six or more individuals was considered "common." This is not many, and it would be entirely inadequate for any quantitative study; but that number was arbitrarily selected as the basis for making a relative comparison. Of the thirty-four species found in numbers sufficient that they may be described as "common," twenty-two are stenozonal and found in only one zone. Eighteen of these were in the plains, one in the foothills, and three in the montane zone.

Six species were collected from two zones: four in both plains and foothills, and one each in foothills-montane, montane-subalpine, and subalpine-alpine. The number of species found in three zones, or that might be so

TABLE 2.—Number of species in each zone

Zones	Number of species
Plains only	52
Foothills only	10
Montane only	18
Subalpine only	1
Alpine only	0
Plains-foothills	5
Plains-montane	3
Foothills-montane	1
Montane-subalpine	1
Subalpine-alpine	1
Montane-alpine	2
Plains-alpine	2
Plains-foothills-montane	1
Plains-montane-alpine	1
Foothills-subalpine-alpine	1
Montane-subalpine-alpine	1
Total	100

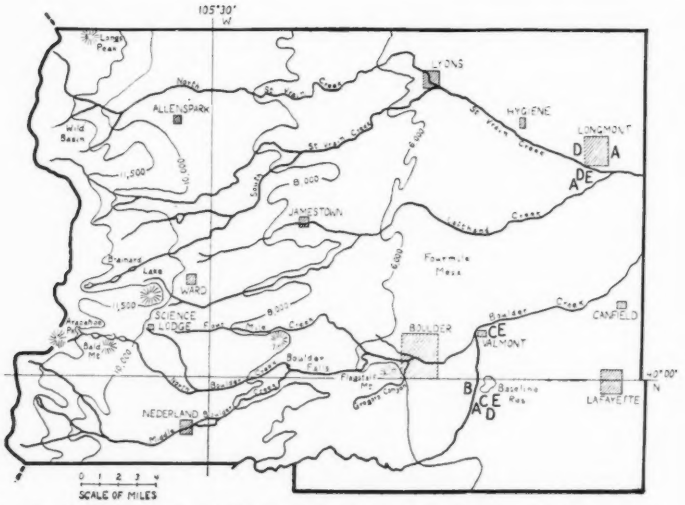

Fig. 4.—Distribution of *Chlaenius diffinis* (A); *C. impunctifrons* (B); *C. pennsylvanicus* (C); *C. sericeus* (D); *C. tricolor* (E).

implied since the zones in which they were collected are not adjacent, was five. One species, *Harpalus seclusus* Casey, collected in the foothills, the subalpine, and the alpine zones was most widely distributed. Of the other four species, one was found in the plains, foothills, and montane zones; one in the montane, subalpine, and alpine; and two, taken in the montane and alpine zones, ought also to be found in the subalpine zone (fig. 5).

In the three highest zones (montane, subalpine, and alpine), twenty-six species of Carabidae were collected which were not found at lower levels. Twenty-two were in the montane zone and 18 of these were limited to that area.

The diagnostic species for the various zones are given in table 3 and they are also plotted on the map (fig. 6). Dominant species seemed to be most distinct in the plains and montane zones. Nine species, limited to the plains zone, were common there; and there were three species characteristic of the montane zone. Eight of the nine plains forms were found in very wet habitats and may be classed as hydrophiles. The ninth, *Agonoderus comma* (Fabr.), was present in a more arid environment.

TABLE 3.—Zonal distribution of dominant species

Plains:	Key to map (Fig. 6)
Agonoderus comma (Fabr.)	A
Brachinus cordicollis Dej.	B
Chlaenius impunctifrons Say	C
C. pennsylvanicus Say	D
C. sericeus Forst.	E
Platynus extensicollis (Say)	F
P. melanarius (Dejean)	G
Tachyura dolosa (Leconte)	H
T. incurva (Say)	J
Foothills:	
Bembidion scopulinum (Kirby)	K
Montane:	
Celia scolopax Casey	L
Pristodactyla advena (Leconte)	M
Pterostichus protractus Lec.	N
High altitudes:	
Bembidion incertum (Mots.)	P
Calathus coloradensis Casey	Q
Cymindis unicolor Kirby	R
Pterostichus lecontellus Csiki	S

The one species taken in the foothills only, was neither abundant nor widely distributed and probably should not be considered a true dominant or characteristic form although it has been included in the table. Neither were there distinctive species for the subalpine or alpine zones. Species which seem to be characteristic of high altitudes, without respect to zonal limits, have been listed.

A number of species, which are not in the collection for this study, are to be found in Boulder County according to previous records. These should be included in a list of Boulder County Carabidae, although the exact locality where most of the species were collected is unknown. Table 4 on page 699 gives these additional records.

In addition to the specimens collected in Boulder County, there are in the writer's collection a number of individuals belonging to four different genera which were collected by Dr. and Mrs. R. E. Gregg in areas outside the County, but sufficiently near that we should expect to find those species here also.

One of the species (*Carabus taedatus patulicollis* Casey) was found in the alpine zone on Mt. Evans southwest of Denver, and at 11,600 feet near Iceberg Lake in Rocky Mountain National Park.

The other three, *Cryobius hudsonicus* Leconte, *Curtonotus brunnipennis* Dejean, and *Cymindis acomana* Casey, were found on Fall River Pass at 12,000 feet. The species of *Carabus* and *Cryobius* were found in the

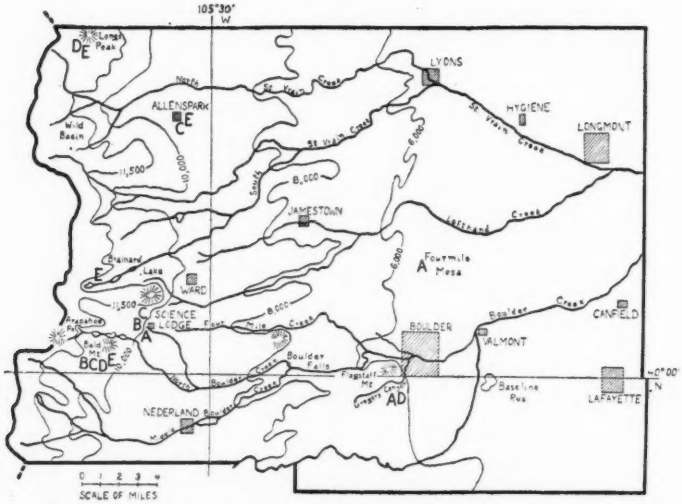

Fig. 5.—Distribution of euryzonal forms. *Bothriopterus saxatilis* (A); *Carabus taedatus oregonensis* (B); *Cymindis unicolor* (C); *Harpalus seclusus* (D); *Pterostichus lecontellus* (E).

montane zone in Boulder County, but not in the alpine zone. The latter two species, *Curtonotus brunnipennis* and *Cymindis acomana*, are not represented in the Boulder County collection at all. C. *brunnipennis* is listed by Van Dyke (1921) from the "high mountains of Colorado."

TABLE 4.—Additional Boulder County Records

Species	Locality	Source
Agonoderus pallipes Fabr.	Foothills	Rodeck, 1929
Agonoderus pallipes Fabr.	"Boulder"	Univ. Museum
Amara laurana Casey	"Boulder Co."	Notman, 1918
A. (*Celia*) *terrestris* Lec.	"Boulder"	Univ. Museum
Bradycellus californicus Leconte	Ward—9000'	Cockerell, 1905
Cymindis cribrata Lec.	"Boulder"	Univ. Museum
Dicaelus sculptilis Say	Foothills	Rodeck, 1929
Dicaelus sculpturatus	"Boulder"	Univ. Museum
Geopinus incrassatus Dej.	"Boulder"	Univ. Museum
Lebia atriceps Leconte	"Boulder"	Univ. Museum
Patrobus septentrionalis DeGeer	Foothills	Rodeck, 1929
Platynus cupripennis Say	"Boulder"	Univ. Museum
Platynus funebris Lec.	Foothills	Rodeck, 1929
Pterostichus (*erythropus* DeGeer) ?	Foothills	Rodeck, 1929

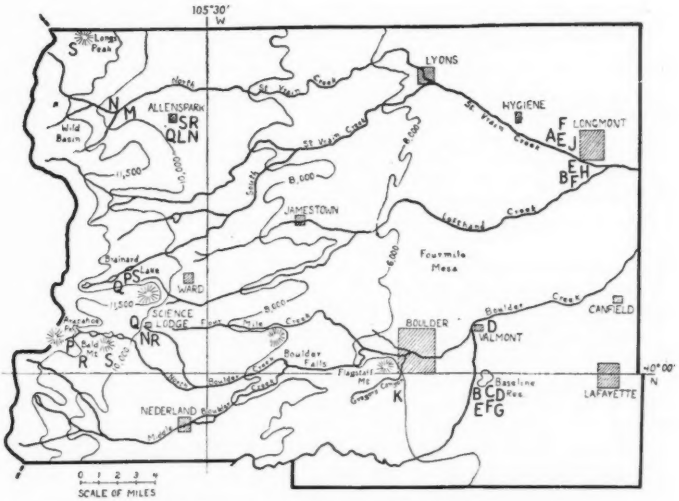

Fig. 6.—Distribution of the dominant species in each zone (see Table 3).

ANNOTATED LIST OF SPECIES

Agonoderus comma (Fabr.).—Flying along the road in large numbers and under roadside debris in the plains zone. Station 3.

New Hampshire (Darlington, 1943).

Agonoderus obliquulus Casey.—From roadside debris in the plains zone, at stations 3, 4.

Fort Collins, Colorado; Jemez Springs, New Mexico; Provo, Utah (Casey, 1914).

Amara cupreolata Putzeys.—Under debris, plains zone. On the walks of the University of Colorado campus in large numbers during July and August. Stations 3, 10.

Mountains of New Hampshire (Darlington, 1943).

Amara fallax Leconte.—Plains zone; under debris along creek banks and on Fourmile Mesa north of Boulder. Stations 3, 8, 9.

Florissant, Colorado (Bowditch collection, Leconte, 1878). Casey (1918) says the species extends from Ontario and North Carolina westward to Boulder County and that it may be found in the sub-arctic.

Amara impuncticollis Say.—One specimen found under debris at station 3.

Old Pecos Pueblo, New Mexico (Fall and Cockerell, 1907). Foothills near Boulder (Rodeck, 1929). The Presidential Range, New Hampshire (Darlington, 1943).

Amara lecontei Csiki [= *polita* Leconte].—Plains zone: many flying along the road; others under debris along a creek. Montane zone: under debris in an open woods on a south slope. Stations 3, 9, 18.

Buford, Colorado (Cockerell, 1909). Various places in New Mexico (Fall and Cockerell, 1907). Colorado, Lake Superior, Adirondack Mountains (Notman, 1918). Presidential Range (Darlington, 1943).

Anisodactylus harrisi Leconte.—In roadside debris, plains zone. Station 3.

Sacramento Mountains, New Mexico (Fall and Cockerell, 1907). Presidential Range (Darlington, 1943).

Apristus subsulcatus (Dejean).—One specimen found in wet sand along a creek at 5000 feet. Station 5.

Las Vegas and Hot Springs, New Mexico (Fall and Cockerell, 1907). La Veta, Colorado (E. A. Schwarz collection, Leconte, 1879).

Bembidion bifossulatum (Leconte).—In wet sand along a creek bank in the plains. Station 5.

La Veta, Alamosa, and Garland, Colorado (Schwarz collection, Leconte, 1879). Luna, New Mexico (Fall and Cockerell, 1907). Along rivers and streams in Zion National Park (Tanner, 1928). At 7500 feet in the La Sal Mountains, Utah (Tanner and Hayward, 1934).

Bembidion consanguineum Hayward.—In canyon bottoms of the foothills at stations 12, 14.

Along rivers and streams in Zion National Park (Tanner, 1928).

Bembidion coxendix Say.—In wet sand along a creek in the plains zone. Station 5.

Albuquerque and Thornton, New Mexico (Fall and Cockerell, 1907).

Bembidion dubitans (Leconte).—One specimen found along a creek in the plains zone. Station 9.

In the Sacramento Mountains and at Coolidge, New Mexico (Fall and Cockerell, 1907). South of Flagstaff, Arizona at 6000 feet (Snow, 1904).

Bembidion incertum (Motschulsky).—Between Lake Isabelle and Long Lake in the subalpine zone, at station 20. Above timber-line on Bald Mountain, at station 23.

In the subalpine zone at the top of Las Vegas Range (Fall and Cockerell, 1907). Van Dyke (1919a) says this species is characteristic of the Hudsonian zone of the Pacific coast, and Hamilton (1894) lists it in his *Catalogue of the Coleoptera of Alaska.*

Bembidion lucidum (Leconte).—In wet sand at station 5 in the plains and near Boulder Falls, station 15.

Garland and Florissant, Colorado (Leconte, 1878). Along streams and rivers in Zion National Park according to Tanner (1928). In Alaska (Hamilton, 1894). Fall and Cockerell (1907) say the species is characteristic of the foothills and montane zones. The University of Colorado Museum has a specimen labeled "Boulder."

Bembidion nitidum (Kirby).—Under debris at station 8 in the plains zone.

Notman (1918) includes it in his list of carabids found at high altitudes.

Bembidion patruele Dejean.—Under debris at station 6 and in wet sand at station 5.

Notman (1920) lists it from Windsor, N. Y., and the Bowditch collection contains specimens from above Georgetown, Colorado (Leconte, 1878).

Bembidion scopulinum (Kirby).—On the south-facing slope in Gregory Canyon, station 12.

At 4000 feet in the La Sal Mountains (Tanner and Hayward, 1934). Glacial relict in the Presidential Range (Darlington, 1943). Alexander (1940) also lists it as an evident Arctic-Alpine form in the same Range. Notman (1918) says there are extensive records of it at high altitudes.

Bembidion stabile (Leconte).—On the south-facing slope of the canyon at station 12.

At 7000 feet at La Veta, Colorado (Leconte, 1879).

Bembidion timidum (Leconte).—One specimen, under wet newspaper at station 3.

Bothriopterus laxicollis Casey.—On a south-facing slope in open woods of the montane zone at station 18.

Casey (1913) reports it in Colorado, but there is no locality given.

Bothriopterus saxatilis Casey.—In debris on Fourmile Mesa, in Gregory Canyon, and near Science Lodge—stations 8, 12, 17.

Casey (1913) says the species is to be found in the Rocky Mountains from Arizona to Idaho and is especially abundant in Boulder County, Colorado.

Brachinus ballistarius Leconte.—One specimen was found near an irrigation reservoir at 6000 feet near station 16.

Distribution is from New York to New Mexico (Leng and Mutchler, 1933).

Brachinus cordicollis Dejean.—In very wet debris along creek at station 5 and in the cattails at station 11.

Leng and Mutchler (1933) give its distribution as "the United States" which would indicate a very widely distributed species.

Brachinus cyanipennis Say.—In damp sand and debris along creek bank at station 5. Also taken with molasses bait trap in the same area.

Brachinus medius Harris.—One specimen was found in the cattail swamp at station 11.

Brachinus minutus Harris.—One specimen, found in debris washed ashore by high water at station 5.

Bradytus latior Kirby.—At station 14 in Boulder Canyon and on a south-facing slope in an open area of the montane zone at station 18.

Calathus coloradensis Casey.—Under debris at stations 17 and 18 in the montane zone, and at station 20 in the subalpine zone.

Reported in Boulder County by Casey (1913).

Calosoma calidum Fabr.—At edge of swampy area near station 5.

Windsor, New York (Notman, 1920). Las Vegas, New Mexico (Fall and Cockerell, 1907). Mountains in New Hampshire (Darlington, 1943)

Carabus serratus tatumi Motschulsky.—One specimen only. In canyon bottom at station 16, foothills zone.

Hudson Bay area (Casey, 1913). Santa Fe Canyon and Las Vegas, New Mexico (Fall and Cockerell, 1907). In both mountains and lowlands in vicinity of the Presiden-

tial Range (Darlington, 1943). Hudson Bay Territory and Newfoundland (Blackwelder, 1939).

Carabus taedatus oregonensis Casey [form *montanicus*].—Under debris at Science Lodge (station 17) and under rocks in the alpine zone at station 23.

Top of Las Vegas Range and from Cloudcroft, New Mexico (Fall and Cockerell, 1907). *Carabus oregonensis* is recorded from montane, subalpine, and alpine zones of the Medicine Bow Mountains (Blake, 1945). *Carabus taedatus*, with no sub-species given, was collected above timberline on Mt. Rainier (Melander, 1921); on Argentine Pass at 13,000 feet (Bowditch collection, Leconte, 1878); Atlanta, Idaho (Leconte, 1878); Buford, Colorado (Cockerell, 1909); at 6000 and 9500 feet near Flagstaff, Arizona (Snow, 1904); and in Alaska (Hamilton, 1894).

Carabus taedatus patulicollis Casey.—Under debris on south-facing slope, station 18.

Collected at 11,600 feet near Iceberg Lake in Rocky Mountain National Park by E. V. Gregg in 1945, and at 12,470 feet on Mt. Evans southwest of Denver, Colorado, by R. E. Gregg in 1947. These specimens are in the author's collection.

Celia ellipsis Casey.—Along roadside at stations 2, 3, and 7 in the plains zone and under debris at station 17 in the montane zone.

Celia farcta Leconte.—Flying in large numbers along roadsides on April 19 and 20, 1947 at station 3.

Jemez Springs, Santa Fe, and Fort Wingate, New Mexico, and Boulder County, Colorado (Casey, 1918).

Celia museulus (Say).—Open areas in the montane forest at station 17.

Celia scolopax Casey.—Very numerous under debris on south slopes at station 18.

Eldora, Boulder County, Colorado in the montane zone (Casey, 1918).

Celia thoracica Casey.—Under debris on south slopes at station 18.

Casey (1918) reports it in Boulder County.

Chlaenius diffinis Chaudoir.—At stations 4, 5, and 11 in the plains zone: under debris, in wet sand, and in cattail swamp.

Chlaenius impunctifrons Say.—Very numerous in cattail swamp at station 11.

Chlaenius pennsylvanicus Say.—In debris washed up at edge of sand pit at station 9 and in cattail swamp at station 11.

Las Vegas and Albuquerque, New Mexico (Fall and Cockerell, 1907). Alamosa, Colorado (Leconte, 1879). Presidential Range (Darlington, 1943).

Chlaenius sericeus Forst.—Abundant in moist areas of the plains zone, at stations 3, 5, 11. Several were found in the molasses traps.

Las Vegas, New Mexico and the top of Las Vegas Range (Fall and Cockerell, 1907). Alamosa, Colorado (Leconte, 1879). Green River City, Wyoming (Bowditch collection, Leconte, 1878). At 4000 feet in the La Sal Mountains in Utah (Tanner and Hayward, 1934). Zion National Park (Tanner, 1928).

Chlaenius tomentosus (Say).—Collected in Sunshine Canyon in the foothills northwest of Boulder in 1944 by R. E. Gregg and in the writer's collection.

Chlaenius tricolor Dejean.—Moist habitats in the plains: cattail swamp, edge of sand pit, creek bank. Stations 5, 9, 11.

Specimen labeled "Boulder" is in the University of Colorado Museum. Albuquerque (Fall and Cockerell, 1907). La Sal Mountains (Tanner and Hayward, 1934). Presidential Range (Darlington, 1943).

Cratacanthus dubius (Beauvois).—Under wet newspaper along road at station 3 and under debris where there was some moisture at station 8 on Fourmile Mesa.

La Veta, Colorado at 7000 feet (Schwarz collection) and Garland, Colorado at 8000 feet (Bowditch collection). Coolidge, Cloudcroft, and Mesilla Park, New Mexico (Fall and Cockerell, 1907).

Cryobius hudsonicus Leconte.—In debris in open area of montane forest at station 17.

One specimen in the writer's collection was collected by E. V. Gregg at Fall River Pass, altitude 12,000 feet. Notman (1918) reports it in the Lake Superior region, in the mountains of New Hampshire, and above timber-line in Hudson Bay Territory. An evident Arctic-Alpine form according to Alexander (1940).

Cryobius mandibularis (Kirby).—One specimen found along the trail in Wild Basin, station 19.

Reported from latitude 54° North (Notman, 1918) and in the Presidential Range (Alexander, 1940 and Darlington, 1943).

Cryobius riparius (Dejean).—One specimen found in the camp area at Science Lodge, station 17.

Curtonotus carinatus (Leconte).—One specimen from the cattail swamp, station 11.

Curtonotus laticollis (Leconte).—Under debris at stations 2, 5.

Cymindis unicolor Kirby.—Under debris on generally south-facing slopes in the montane zone at stations 17, 18 and under rocks in the alpine zone, station 23.

The Bowditch collection contains many specimens found between 9000 and 13,000 feet in the Colorado Rockies (Leconte, 1878). Other records are from Labrador and New England, and Argentine Pass, Colorado (Sherman, 1910), and as a glacial relict in the Presidential Range (Darlington, 1943). An evident Arctic-Alpine species in the Presidential Range (Alexander, 1940).

Eumolops sexualis Casey.—Abundant throughout the plains and in the canyon bottoms of the foothills. Stations 1-7, 9, 16.

Casey (1918) reports it at Las Vegas, New Mexico. Specimens collected in Sunshine Canyon northwest of Boulder and on Haystack Mountain near Niwot by R. E. Gregg are in the writer's collection.

Harpalus amputans Say.—Under debris at stations 3, 4, 6.

Under the synonym, *Harpalus amputatus,* the species is reported between 8000 and 10,000 feet in the Colorado Rockies by Leconte (1878); at Alamosa and Garland, Colorado (Leconte, 1879); at 6000 feet and 9500 feet near Flagstaff, Arizona (Snow, 1904); and in Zion National Park (Tanner, 1928).

Harpalus caliginosus (Fabr.).—Creek banks and canyon bottoms and on Flagstaff Mountain: stations 9, 13, 14, 16.

A specimen from the Boulder Mesa, bordering the foothills is in the University Museum. Fall and Cockerell (1907) found it in the Upper Sonoran and Transition zones of New Mexico.

Harpalus cautus Dejean.—One specimen found under the debris at station 18.

Coastal California and Clackamas County, Oregon (Casey, 1914).

Harpalus compar Leconte.—Along creeks, under debris at stations 9, 16.

Windsor, New York (Notman, 1920). Santa Fe Canyon (Fall and Cockerell, 1907).

Harpalus curticornis Casey.—One specimen found under a stone along the stream in Gregory Canyon (station 12).

Collected at Salida, Colorado (Casey, 1914).

Harpalus erraticus Say.—One specimen, in debris washed up by high water at station 5.

Harpalus furtivus Leconte.—One specimen taken at station 18.

Reported at Eldora, also in the montane zone of Colorado, by Casey (1914). At timber-line in the La Sal Mountains (Tanner and Hayward, 1934).

Harpalus herbivagus Say.—Along roadsides, under vegetation washed up by high water, under logs in wooded area along creek, and on the walks on the University campus (stations 2, 3, 5, 6, 9, 10).

At 9500 feet near Flagstaff, Arizona (Snow, 1904). Alma and South Park, Colorado (Bowditch collection, Leconte, 1878). From plains and foothills in New Mexico (Fall

and Cockerell, 1907). Presidential Range (Darlington, 1943) and Labrador (Sherman, 1910).

Harpalus lustrans Casey.—One specimen, under bark of a tree stump at station 17.

Distributed from Wyoming to Arizona according to Casey (1914). Santa Fe, Albuquerque, and Coolidge, New Mexico (Fall and Cockerell, 1907).

Harpalus pennsylvanicus DeGeer.—Found under bricks bordering a garden, along a road, and one was found in a dwelling house at night, at stations 2, 6, 10.

Plains zone in New Mexico (Fall and Cockerell, 1907). Zion National Park (Tanner, 1928). In Arizona at 1000, 6000, and 9500 feet (Snow, 1904). Presidential Range (Darlington, 1943). Casey (1914) says it extends westward to Boulder County.

Harpalus pleuriticus Kirby.—Under bits of wood at station 9.

Alamosa, Colorado (Leconte, 1879). Windsor, New York (Notman, 1920). Vermont (Casey, 1914) Presidential Range (Darlington, 1943).

Harpalus probatus Casey.—One specimen on the University campus, at station 10.

Jemez Springs, New Mexico and an unidentified locality in Colorado (Casey, 1914).

Harpalus seclusus Casey.—In the canyon bottom at station 12, above timberline at station 22, and in both alpine and subalpine zones at station 23.

Casey (1914) reports it from Colorado, but no locality is given.

Harpalus sejunctus Casey.—Found in debris deposited by high water at station 5.

Eldora, Colorado, in the montane zone in Boulder County (Casey, 1914).

Loricera pilicornis Fabr. [= *caerulescens* L.].—Along a road and in the cattail swamp at stations 3, 11.

Reported from high altitudes or northern latitudes by Notman (1918), Tutt (1902), Lindberg (1927), Hamilton (1894), Sherman (1910), Darlington (1943), and Alexander (1940).

Melanius [= *Omaseus*] *caudicalis* (Say).—In roadside debris at station 3. One specimen.

Leng and Mutchler (1933) list it from New Jersey, Virginia, and Oregon.

Melanius corvinus Dejean.—One specimen in the cattail swamp at station 11.

Reported from New York, Georgia, and the Lake Superior region (Leng and Mutchler, 1933).

Melanius luctuosus (Dejean).—Under rocks along the railway and in the cattail swamp, stations 4, 11.

Newfoundland, Virginia, and Illinois (Leng and Mutchler, 1933).

Metabletus americanus (Dejean).—In wet sand and debris at station 5 and under rocks at station 18.

Plains and lower montane zones in New Mexico (Fall and Cockerell, 1907). At 8000 and 9400 feet in southern Colorado (Leconte, 1879). Both mountains and lowlands in New Hampshire (Darlington, 1943).

Nebria obtusa Leconte.—Found at the foot of Arapahoe glacier (station 21) and on the creek bank at station 9.

Van Dyke (1926) lists it as a high altitude form with distribution from Alberta, Canada to Colorado. The Bowditch collection contains specimens taken at 6000-7000 feet along the South Platte River (Leconte, 1878). Provo, Utah (Casey, 1913).

Nebria purpurata Leconte.—Along the shores of Lake Isabelle at the upper edge of the subalpine zone, station 20.

Mountains of Idaho and Colorado (Van Dyke, 1926). Above Georgetown, Colorado (Leconte, 1878).

Nothopus zabroides Leconte.—One specimen was found on the Flagstaff road, station 13.

Plains and foothills of New Mexico (Fall and Cockerell, 1907). El Paso, Texas and an unidentified locality in Colorado (Casey, 1914).

Omaseulus [= *Micromaseus*] *desidiosus* (Leconte).—Under stones and wood at station 3.

Pasimachus elongatus Leconte.—Under stones at station 1 and in ditches cut by erosion at station 8.

Santa Fe and Las Vegas, New Mexico (Fall and Cockerell, 1907). At 7000 feet in southern Colorado (Leconte, 1879). Foothills near Boulder (Rodeck, 1929). The University Museum has a specimen labeled "Boulder."

Patrobus longicornis (Say).—Under rocks near the streams at stations 12 and 14 in the foothills.

At 7000 and 8000 feet in southern Colorado (Leconte, 1879). Sacramento Mountains (Fall and Cockerell, 1907).

Percosia diffinis Leconte.—Under stones at station 2 and in gravel of old creek bed at station 5.

Reported from Denver, Colorado and in Nebraska (Casey, 1918).

Philophuga amoena (Leconte).—One specimen was found at station 18.

Near Longs Peak (Casey, 1913) and the plains at the base of the Medicine Bow Mountains (Blake, 1945).

Platynus affinis (Kirby).—One specimen taken at station 18.

Taos, New Mexico (Fall and Cockerell, 1907). Presidential Range (Darlington, 1943).

Platynus decorus (Say).—One specimen from station 11.

At Albuquerque and in the Mesilla Valley in New Mexico (Fall and Cockerell, 1907).

Platynus extensicollis (Say).—Very abundant, especially in wet places. At stations 3, 5, 11. Taken with bait traps at station 5.

Windsor, New York (Notman, 1920) and Mesilla, New Mexico (Fall and Cockerell, 1907).

Platynus melanarius (Dejean).—Abundant in the cattail swamp at station 11.

Windsor, New York (Notman, 1920).

Platynus placidus (Say).—Widely distributed throughout the plains. At stations 3, 4, 6, 8, 9, 10, and in bait trap at 5.

Reaches the lower edge of the montane zone in New Mexico (Fall and Cockerell, 1907). At 8000 feet in southern Colorado (Bowditch collection, Leconte, 1878). Presidential Range (Darlington, 1943).

Platynus seminitidus Kirby.—In the montane zone at stations 17, 18.

Poecilus lucublandus Say.—Has a wide distribution in the plains zone. Found at stations 3-6, 11.

Both lowlands and mountains in New Hampshire (Darlington, 1943).

Pristodactyla advena (Leconte).—Under rocks at station 19 on May 30, 1947. Most of the specimens were inactive, but those which were not often escaped into ant tunnels which were usually present under the same rocks.

Above 3000 feet in the Presidential Range (Darlington, 1943).

Pterostichus lecontellus Csiki [= *longulus* Leconte].—Abundant in the montane, subalpine, and alpine zones at stations 18, 20, 22, 23.

Colorado records: 10,500 feet on Trail Ridge Road in Rocky Mountain National Park by R. E. Gregg (writer's collection); Buford (Cockerell, 1909); Leadville and Eldora (Casey, 1913); Georgetown (Leconte, 1878); and at 8000 and 9200 feet in southern Colorado (Leconte, 1879). Also recorded in the subalpine and alpine zones in the Medicine Bow Mountains (Blake, 1945) and from the plains to the lower montane zone in New Mexico (Fall and Cockerell, 1907).

Pterostichus protractus Leconte.—Montane zone, under debris, both open and forested areas. Stations 17-19.

At 7200 feet in northwestern Colorado (Cockerell, 1909). Montana, Wyoming, and Boulder County, Colorado (Casey, 1913). Santa Fe Canyon, New Mexico (Fall and Cockerell, 1907). Zion National Park (Tanner, 1928). Atlanta, Idaho (Leconte, 1878). Characteristic of the montane zone in the Cascades and Sierras (Van Dyke, 1919a).

Rembus obtusa Leconte.—One specimen found on the walk on the University campus, station 10.

Scaphinotus elevatus coloradensis Van Dyke.—Under stones near stream at station 12. Found in Colorado, New Mexico, and Nebraska according to Leng and Mutchler (1933).

Selenophorus [*Selenophorus*] *pedicularius* Dejean.—Stations 10, 23, University campus and alpine zone on Bald Mountain. One specimen from each station.

At 3000 feet at Martinez, Arizona (Snow, 1904). Numerous points in New Mexico (Fall and Cockerell, 1907).

Selenophorus [*Selenophorus*] *planipennis* Leconte.—Along stream in the canyon bottom at station 12.

Casey records it from Boulder County without giving the exact locale (1914).

Stenocellus rupestris (Say).—In very moist habitats at stations 3, 5.

Presidential Range (Darlington, 1943).

Stenocellus tantillus (Dejean).—Under bits of wood at stations 17, 18.

Stenolophus conjunctus (Say).—Stations 3, 5. One specimen at each.

One specimen labeled "Boulder" is in the Museum at the University of Colorado. At 8000 feet at Florissant, Colorado (Bowditch collection, Leconte, 1878). Zion National Park (Tanner, 1928). Beulah, Coolidge, and San Geronimo, New Mexico (Fall and Cockerell, 1907). Presidential Range (Darlington, 1943).

Stenolophus fuliginosus Dejean.—One specimen among the cattails at station 11.

Above 3000 feet in the Presidential Range in New Hampshire (Darlington, 1943).

Tachyura dolosa (Leconte).—Very numerous in the damp sand of the creek bank at station 5.

Tachyura incurva (Say).—Under debris where it was quite moist, station 3.

Throughout the eastern United States according to Casey (1918). Presidential Range (Darlington, 1943).

Triplectrus rusticus (Say).—Under rocks at stations 2, 17, 23. Only one specimen at each station.

Rhode Island to Arizona (Casey, 1914). Presidential Range (Darlington, 1943).

Trechus chalybeus saxatilis Casey.—A single specimen found under a rock on the moraine above Science Lodge at station 17.

Siskiyou County, California; Vancouver Island; and Unalaska Island (Casey, 1918). New Mexico (Fall and Cockerell, 1907). Alaska (Hamilton, 1894).

SUMMARY

This paper is the result of a study made during 1946 and 1947 to determine the zonal distribution of the species of Carabidae in Boulder County, Colorado.

The five established life zones in the County are plains, foothills, montane, subalpine, and alpine. These zones are represented by a total of twenty-three collecting stations.

Six hundred twenty-seven specimens representing 41 genera and 100 spe-

cies were collected. In addition, there are included the records of a number of species taken by Dr. and Mrs. R. E. Gregg in 1944 and 1945 and those previously published records which have come to the author's attention.

There is definite evidence that vertical zonation among the Carabidae does exist in Boulder County as indicated by the fact that 22 of the 34 most common species in the collection were found in only one zone.

Characteristic species of the plains were *Agonoderus comma* (Fabr.), *Brachinus cordicollis* Dej., *Chlaenius impunctifrons* Say, *C. pennsylvanicus* Say, *C. sericeus* Forst., *Platynus extensicollis* (Say), *P. melanarius* (Dejean), *Tachyura dolosa* (Leconte), and *T. incurva* (Say). In the foothills, one species, *Bembidion scopulinum* (Kirby), was listed as characteristic, but it was not a strong dominant. *Celia scolopax* Casey, *Pristodactyla advena* (Leconte), and *Pterostichus protractus* Leconte were diagnostic of the montane zone; and *Bembidion incertum* (Mots.), *Calathus coloradensis* Casey, *Cymindis unicolor* Kirby, and *Pterostichus lecontellus* Csiki were distinctly characteristic of high altitudes.

The number of species decreased as altitude increased and the occurrence of individuals was noticeably less frequent.

There were nineteen euryzonal forms extending over two or more life zones, but this does not disprove zonation. The presence of similar environmental conditions in the various zones probably accounts for their wider distribution.

Bembidion incertum (Motschulsky) and *Nebria purpurata* Leconte were the only two species collected in Boulder County which were not found in the montane zone or lower.

There was an extension downward into the montane zone of the species which, according to the literature consulted, are high altitude forms. *Cryobius hudsonicus* Lec., *Cryobius mandibularis* (Kirby), and *Cymindis unicolor* Kirby were in this group. One specimen of *Nebria obtusa* Leconte, another reportedly high altitude species, was found in the plains zone, although possibly as an accidental.

Plains forms extended into the foothills if they found similar habitats there or if they inhabited a variety of environments in the plains zone. This tendency was present although less marked among species which crossed other zonal boundaries. Therefore zonation tended to disappear where similar habitats made it possible for the species to extend its range.

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Studies on Metacercariae of Perca flavescens in Lake Itasca, Minnesota*

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Examination of large numbers of perch of various ages from Lake Itasca, Minnesota, revealed infestation by eight different species of metacercaria, including five, marked by asterisks in the following list, not hitherto reported from this host, four of these representing new species:

Diplostomulum scheuringi
Neascus bulboglossus
* *Neascus pyriformis* n. sp.
* *Neascus longicollis* n. sp.
* *Neascus ellipticus* n. sp.
Clinostomum marginatum
* *Cryptogonimus chyli*, new host record
* *Apophallus* sp.

It will be noted that neither *Neascus vancleavei* nor *N. ambloplitis* are included, although both have been reported from this host in other localities, and both are common in the rock bass, *Ambloplites rupestris*, and other Centrarchidae in this lake. *Neascus pyriformis* rather closely resembles *N. ambloplitis*, and *N. ellipticus* closely resembles *N. vancleavei*, and it may be possible that these new species have at times been misidentified as representatives of the others.

Below are notes on the occurrence of these various parasites with descriptions of the new species of strigeid metacercariae, and of the hitherto imperfectly known metacercaria of Cryptogonimus.

Neascus bulboglossus

This metacercaria, a well known and widely distributed form, the larva of a kingfisher parasite, *Crassiphiala bulboglossa*, was found in about 40% to 50% of the perch in Lake Itasca, but only occasionally in very large numbers. It was nearly always found in association with *Neascus pyriformis*, described below, but the latter form was found in about 95% of the perch in the lake. These two species are the cause of nearly all of the "blackspots" in the skin and fins of perch. The only other type of blackspot found in the skin was caused by the relatively rare cysts of *Neascus longicollis* n. sp., described below. When *N. pyriformis* and *N. bulboglossus* occurred together, *N. bulboglossus* only rarely predominated, and often constituted only 5% to 20% of the blackspots present. Both species have rather tough double-contoured parasite cysts which lie loosely inside of the thick fibrous hosts cysts, the latter, in turn, surrounded by more or less densely packed pigment cells, which, however, do not often form as large or diffused spots as do those of *N. ambloplitis* in the flesh and fins of members of the bass family. If the pigment cells are scraped away from the host cysts the shape of the parasite cysts

* Contribution from University of Minnesota Biological Station and Rice Institute.

inside can usually be seen without trouble, and the cysts of *N. bulboglossus* easily distinguished from those of *N. pyriformis* by their evenly rounded contour as compared with the pyriform shape of the *N. pyriformis* cysts. The parasite cysts of both species can very easily be popped out from the host cysts by pressure on a coverglass. It is very difficult to crack the parasite cysts of either species even with considerable pressure on a cover glass, and it is difficult to free the parasites from the cysts for detailed study and measurement. No success was obtained from the use of either artificial gastric juice or trypsin, although Hughes (1928b) stated that the parasite cysts open readily in a warm bath of trypsin in 0.5% sodium bicarbonate. With patience, however, the parasites can be freed by means of fine needles made from insect pins.

N. bulboglossus was found abundantly also in the walleye, *Stizostedion vitreum,* which belongs to the same family as *Perca flavescens.* In some individuals from Lake Itasca this fish, like the perch, had more blackspots produced by *N. pyriformis* than by *N. bulboglossus,* but in a few walleyes the latter species was the only one present, and this was true of several walleyes and perch examined from Leech Lake, about 30 miles away. Both *bulboglossus* and *pyriformis* were found also in killifish (*Fundulus diaphanus*) but not as frequently or as abundantly as in perch; in this fish *pyriformis* always predominated.

No specimens of *N. bulboglossus* were found in members of the bass family (*Ambloplites rupestris, Huro salmoides, Lepomis macrochirus,* or *Pomoxis nigromaculatus,* nor in numerous other fish, including *Notropis* sp., *Semotilus* sp., silurids, *Catostomus,* or northern pike, *Esox lucius.* This last fish has been reported as a host for *N. bulboglossus* by several writers, including Hunter and Hunter (1929), who reported the cysts as occurring under the scales, just as in perch, and morphologically identical with *N. bulboglossus.* In Lake Itasca and neighboring lakes the northern pike frequently is heavily infested by a blackspot-producing metacercaria that is closely related to *N. bulboglossus* and undoubtedly the larva of a species of *Crassiphiala,* but this metacercaria differs in a number of details, and is invariably found in the skin on *top* of the scales, not under them. In a young belted kingfisher, *Megaceryle alcyon,* obtained when just about ready to leave its nest on the banks of Lake Itasca, among five or six hundreds of specimens of *Uvulifer,* representing two species of that genus, there were found that one hundred specimens of *Crassiphiala,* all of which were at first thought to represent the well-known species, *C. bulboglossa.* Upon closer study, however, it seems probable that two species are represented, one of which is in all probability the adult of the superficially-located *Neascus* of the Northern Pike. A description of this species and its possible adult form will be given elsewhere.

Neascus pyriformis n. sp.

This is the commonest blackspot-producing metacercaria in the skin of perch in Lake Itasca and vicinity. A few very small perch a few months old

and some 8 or 9 inches long from deeper water in the lake were devoid of blackspots on the skin; the parasites were most numerous in young perch about 3 inches long, but occasional specimens 6 to 7 inches long contained 1000 or more blackspots. As noted under *Neascus bulboglossus* above, many perch harbored both that species and *N. pyriformis*, but in Lake Itasca the latter species usually predominated and was frequently the only one present. *N. pyriformis* was also found, sometimes abundantly, in *Fundulus diaphanus* and also in the walleye, *Stizostedion vitreus*. A few were occasionally found in the fins, but not under the scales, of *Ambloplites rupestris*, where they were intermingled with *Neascus ambloplitis*. None were found in either young or old crappies, bluegills or large-mouth bass.

The host cyst is a thick fibrous envelope, varying in size from spheres 400 to 540μ in diameter to ovoid bodies 420 to 550μ long and 300 to 500μ wide. The wall varies from 10μ to 65μ in thickness, and may be more than twice as thick on one side as on another. Outside of the dense fibrous cyst is an accumulation of pigment cells, sometimes forming a complete thin black envelope around the cyst, with gradually more scattered pigment cells extending outward. In many cysts, however, the pigment cells are much less numerous and give a speckled appearance. The host cyst does not closely invest the parasite cyst; the latter floats freely inside, its short diameter often being less than half the diameter of the space in which it floats. The parasite cyst has a very characteristic pear shape which makes it identifiable at once, and easily distinguishable from either *N. bulboglossus* or *N. ambloplitis*, with either of which it may be associated. The parasite cysts measure 225 to 319μ in length and 130 to 195μ in diameter. The narrowed neck at one end is 65 to 72μ across and about 25μ long, frequently with fine circular striations. The cyst is about 7 to 8μ in thickness and very tough. As remarked above, this parasite cyst is easily popped out of the host cyst under gentle pressure, but it cannot be cracked to release the contained parasite even with considerable pressure on a cover glass.

The parasite almost completely fills the cyst except frequently a part of the forebody folded back from the neck of the cyst and tucked into the posterior concavity of the forebody, and with the hindbody sometimes, but not always, bent back from the posterior end.

In parasites freed from the cysts the forebody measures 435 to 465μ in length and 240 to 255μ in width, and the hindbody 150 to 250μ in length and 125 to 175μ in width. The oral sucker is longer than wide, but is longitudinally compressed while in the cyst. In freed parasites it is about 45μ wide anteriorly, 23μ posteriorly, and 70μ long. The pharynx is difficult to see. It lies immediately behind the oral sucker and measures 21 to 23μ long and 17 to 18μ wide. The ventral sucker, smaller than the oral sucker, measures about 38 to 45μ wide and 38 to 40μ long, but inside the cysts it is often more compressed antero-posteriorly. The holdfast organ lies close behind the ventral sucker and measures about 85 to 105μ in length and 80 to 95μ in width. The general pattern of the reserve bladder is similar to that of *N. ambloplitis* and others of its group (e.g., *wardi*,

rhinichthysi, and *bulboglossus*.) The exact pattern could not be observed in parasites still in the cysts, and so few uninjured parasites were extracted from the cysts that a detailed study of the reserve bladder system could not be made. However, as in *N. ellipticus* (see below) the reserve bladder system ends anteriorly at a point well behind the pharynx, and there do not appear to be more than three, possibly four, anterior commisures. From the last of these a posteriorly directed branch becomes the intra-lateral vessel on each side. These are connected with the primary laterals by several commissures, but ultimately rejoin the primary laterals. The dorsal vessel was not observed to have a ring around the ventral sucker, but bypasses this on one side. It then forms a ring around the base of the holdfast, and continues as a median vessel into the hindbody. Both it and the ventral median vessel bifurcate near the anterior end of the hindbody, and each has numerous lateral branches, which are probably semicircular commissural vessels, as described by Hughes (1927) in *N. ambloplitis*. The exact relationships of the dorsal and ventral vessels at the posterior end of the abdomen could not be determined. The granules in the vessels in the hindbody are very fine, 2 to 4μ in diameter, whereas those in the forebody are often 6 to 8μ in diameter.

As noted above, this metacercaria is easily distinguished from all others by the pear shape of the parasite cyst. The host cysts of *N. ambloplitis*, to which *N. pyriformis* seems to be closely related, reach a larger size (up to 1 to 1.5 mm. or even more in length) and are softer and not as sharply demarcated from the surrounding tissue; *pyriformis* cysts when shelled out of the surrounding pigmented envelope appear like little pearls. It is difficult, often impossible, to expel the parasite cysts of *ambloplitis* by pressure on a cover, as compared with the ease with which *pyriformis* and *bulboglossus* cysts escape. The *ambloplitis* parasite cysts are larger than those of *pyriformis* (340 to 420μ by 200 to 225μ in *Ambloplites rupestris* from Lake Itasca) and are slightly smaller and truncated at the anterior end. In the parasites themselves the ceca of *N. ambloplitis* are usually seen easily whereas in *N. pyriformis* they are not in evidence.

It is possible that the adult of *N. pyriformis* is *Uvulifer semicircumcisus*, which was described by Dubois and Rausch (1950) from numerous specimens collected from the intestine of a kingfisher, *Megaceryle alcyon*, in Michigan. In the nestling kingfisher mentioned above in the section on *N. bulboglossus*, which harbored several hundreds of flukes belonging to the genus *Uvulifer* and a hundred or more *Crassiphiala*, the great majority of the uvulifers were *U. semicircumcisus;* the others were identified as *U. ambloplitis*. Dubois and Rausch found along with their numerous *U. semicircumcisus* a few specimens of a *Uvulifer* which they named *U. magnibursiger* n. sp., but which is probably *U. ambloplitis*. The great prevalence of *N. pyriformis* in killifish and young perch, which are commonly fed on by kingfishers, the general resemblance of *N. pyriformis* to *N. ambloplitis*, and the occurrence in great numbers, in a fledgling kingfisher at the same locality, of *Uvulifer semicircumcisus*, a species not hitherto described elsewhere

except from a single Michigan kingfisher, provides some circumstantial evidence for the suggestion made above, that *N. pyriformis* is the metacercaria of *Uvulifer semicircumcisus*.

Neascus longicollis n. sp.

In a small percentage of perch, usually small ones 2 to 4 inches long, a few *Neascus* of a different type, to which the name *Neascus longicollis* is given, were found scattered among specimens of *Neascus pyriformis* and *N. bulboglossus* in the skin under the scales. The parasite causes the formation of blackspots which cannot be distinguished, without closer examination, from those of the two other dermal species of *Neascus*. The host cyst closely invests the parasite cyst, so that, unlike the other species, there appears to be a single cyst wall. The cyst is oval, the outer dimensions being 480 to 640μ in length by 450 to 500μ in diameter. The inner dimensions are about 400 to 500μ by 325 to 400μ. The walls vary in thickness on different sides of the same cyst from 35 to 65μ. The parasite lies loosely inside the cyst, not nearly filling it, the body lying in a horseshoe form, the anterior and posterior ends not meeting. The forebody is 600 to 700μ long with a long slender neck region, expanding posteriorly to a maximum diameter, in the region of the holdfast organ, of 235 to 260μ. The hindbody is a tail-like structure varying from 170 to 270μ in length and from 60 to 120μ in width, narrower at its junction with the forebody than farther back, and attached anterior to the posterior end of the forebody. The anterior end of the body terminates in a mobile, finger or lip-like process at the dorsal side of the oral sucker. From the mouth opening to the tip of the process is about 50 to 55μ. The oral sucker is about 38 to 42μ in diameter, and about the same in length. No pharynx could be seen. The ventral sucker, situated just in front of the holdfast organ, is smaller than the oral sucker, measuring about 30μ in length and 33 to 35μ in width. The very mobile holdfast organ is mushroom-like, the expanded portion measuring about 100 to 110μ in diameter. All measurements, however, are subject to considerable alteration by contraction and expansion of the worms. The reserve bladder system is of the type seen in the *Neascus ambloplitis* group. However, the anterior extent of it is about midway between the ventral sucker and the anterior end of the body. There are three or four anterior commissures between the median dorsal and primary lateral vessels and an additional fine commissure shortly in front of the ventral sucker. An intra-lateral vessel branches off from the most posterior of the anterior commissures and is connected with the primary lateral vessels by a series of commissures. Rows of very fine granules indicated the presence of marginal vessels, but their connections with the rest of the system could not be traced. The median dorsal and ventral vessels in the hindbody each fork not far from the base of this organ, and contain only very fine granules, but their exact course could not be traced.

In the structure of its reserve bladder and in its effect in causing blackspots this parasite resembles the *N. ambloplitis* group, but in the close

association of host and parasite cysts, and freedom of the parasites within the cysts, it more closely resembles the *N. vancleavei* group (see under *N. ellipticus* below).

Neascus ellipticus n. sp.

An elongate, elliptical, almost transparent cyst, without black pigmentation, containing a *Neascus* resembling *N. vancleavei*, was found sparingly in the flesh of *Perca flavescens*. The cyst is 735 to 900μ long and 360 to 500μ in diameter, and consists of a rather thin host cyst, distinctly pointed at one end, which closely fits against the enclosed parasite cyst except for a little space at the pointed end. The inner space in which the parasite lies measures 570 by 340μ in a cyst with outside measurements of 775 by 360μ. The parasite cyst is very thin and flexible, and under pressure tends to back out of the host cyst at the posterior, rounded end. The parasite, which does not nearly fill the cyst, lies freely inside either straight or slightly bent, the head at the pointed end of the cyst. There is a deep constriction separating the forebody from the hindbody. The forebody, shaped like a thin, shallow spoon, in a relaxed state measures about 450 to 540μ in length with a maximum diameter, at about the level of the ventral sucker, of 300 to 325μ. The forebody of a specimen measuring 450μ in length when relaxed could stretch out to a length of about 750μ. The hindbody in relaxed condition is somewhat narrower and much shorter than the forebody, measuring about 240 to 290μ in length and 250 to 290μ in width, and with the posterior end rather pointed. It is very mobile; it can contract until it is about as wide as the forebody and much shorter than wide, and can stretch to a length of 450μ with the width only about half that much.

The oral sucker is very mobile but when relaxed is from 30 to 42μ long and 22 to 30μ wide. It can be protruded prominently at the anterior end of the body. The ventral sucker is much larger than the oral sucker, and wider than long in relaxed specimens, measuring about 46 to 55μ long by 55 to 63μ broad. The holdfast organ lies in the posterior portion of the forebody, its anterior border close behind the ventral sucker; in relaxed specimens it is approximately round and is 100 to 125μ in diameter.

No prepharynx could be observed, even in stretched specimens. In relaxed specimens the elongate pharynx, measuring 25 to 35μ by 17 to 20μ, lies almost entirely dorsal to the posterior part of the oral sucker. There is a short esophagus. The ceca are easily seen in most specimens; they diverge gradually to the level of the ventral sucker, then bow outwards, the lumen broadened and often beaded in appearance, around the holdfast organ, bending mediad again at the junction of fore- and hindbody, and then bowing out again in the hindbody, the tips bending in to approach the copulatory bursa near the posterior end.

The reserve bladder of the excretory system resembles that of *Neascus vancleavei* and *N. ptychocheilus* rather than that of the *N. amblopitis* group. The forebody gives the appearance of being longitudinally striated, due to the arrangement of the longitudinal vessels of the reserve system and

the ceca. There is a median dorsal vessel running from immediately behind the pharynx to the anterior border of the ventral sucker, but this vessel was not seen to cross this organ as it does in *vancleavei* and *ptychocheilus*, although there is a median dorsal vessel across the holdfast organ. The dorsal vessel is flanked by a pair of parallel intra-lateral vessels, which approximately follow the ceca, and these in turn are flanked by a pair of primary lateral vessels. There are three or four anterior commissures connecting the median dorsal vessel with the intra-laterals. Just anterior to the ventral sucker is a very fine commissure connecting the intralaterals, but its relation to the dorsal vessel in this region was not clear. Between the ventral sucker and holdfast is a very coarse posterior commissure between the intra-laterals with a conspicuous knot of granules at the midline, and from which a median stem proceeds posteriorly dorsal to the holdfast. The intra-laterals and primary laterals are connected by numerous commissures and lateral to the primary laterals is a reticulum of vessels as in the other species in this group. The arrangement of vessels in the hindbody was not satisfactorily observed, but it contains the same enlarged vessels with gelatinous bodies described by Hughes (1928a) for *N. vancleavei*.

This *Neascus* is very similar to *N. vancleavei*, and *N. ptychocheilus*, and was at first thought to be one of these, but it differs in a number of respects. The host cysts are thinner and more transparent, and definitely pointed at one end. The hindbody of the parasite is separated from the forebody by a deep constriction, absent in the other species; in some specimens of *vancleavei* the body constricts *anterior* to the ventral sucker, with no separation of the hindbody at all. The hindbody of *N. ellipticus* is relatively larger than that of either *vancleave* or *ptychocheilus*, is always narrower than the forebody, and is conical in shape. In *vancleavei* and *ptychocheilus* in relaxed or contracted specimens the hindbody is as broad as the forebody, and only about half as long as broad, being broadly rounded posteriorly. The forebody of *ellipticus* tapers anteriorly and posteriorly from the region of the ventral sucker, whereas that of *vancleavei*, when relaxed, has almost parallel sides, with a slight if any constriction at the junction of the hindbody, and very little anterior tapering in the middle portion. In *vancleavei* the ventral sucker is twice or nearly twice as large as the oral sucker, and in *ptychocheilus* it is very little larger; in *ellipticus* it is about 1½ times as large. *N. vancleavei* has a short prepharynx visible when the body is stretched, but *ellipticus* does not. The ceca of *ellipticus* are conspicuous, whereas those of *vancleavei* are seldom clearly visible. In *vancleavei* there are minor differences in the reserve excretory system, particularly in the forward extension of branches from the anterior commissure to the sides of the oral sucker. *N. vancleavei* is usually found in the liver of *Ambloplites* and less frequently in other Centrarchidae, and has also been reported from a number of other fish, sometimes attached to the mesenteries, peritoneum, kidney, or heart. Possibly not all of these represent a single species. *N. ptychocheilus* was found in cysts attached to the peritoneum of the body cavity and viscera, and free in the ovaries, of *Notropis deliciosus* and in the mesenteries of *Ptychocheilus oregonensis*. *N. ellipticus* has so far been found only in

the flesh of *Perca flavescens*. It seems possible that *N. ellipticus* may be the larva of some species of *Neodiplostomum*.

DIPLOSTOMULUM SCHEURINGI

This elongate diplostomulum, of which the adult has not yet been determined, was found in a very high percentage of the perch whose eyes were examined, varying in number from only two or three to about 25 or 30 specimens per eye. As was reported by Hughes (1929), the parasites occur only in the humors of the eye, never in the lens. Concerning this species Mueller and Van Cleave (1934) wrote as follows: "We have found diplostomulids from yellow perch representing a perfectly intergrading series from the *Diplostomulum huronense* (?) usually found in that host, to the *D. scheuringi* type occasionally present. Against the fact that such a series may be natural rests the manner in which *D. scheuringi* occurs. If our series were really a growth series one should expect at times to find a massive infestation with *D. scheuringi* comparable to the heavy infestations with *D. huronense* in perch, but such never occurs." They report pure infestations with this species in several other fish, in some of which *D. huronense* has never been found. The intermediate forms were found only in perch and were very rare, so they rejected a view they set forth in an earlier abstract (Mueller and Van Cleave, 1931) that *D. scheuringi* and *D. huronense* are identical species. This conclusion is fully corroborated by the findings in perch from Lake Itasca where only pure infestations with *D. scheuringi* have been found. The absence of *Diplostomulum huronense*, which develops into *Diplostomum huronense* in gulls, may be correlated with a scarcity of gulls in this lake, at least in the summer months.

CLINOSTOMUM MARGINATUM

The metacercariae of this worm, commonly known as "yellow grubs," are very common in perch in Lake Itasca, this being the commonest host for this parasite. Fish of medium size, 3 to 5 inches in length, usually, though not always, have the heaviest infections. These yellow grubs are so common and conspicuous in perch in this lake that these fish are not considered fit for food.

CRYPTOGONIMUS CHYLI

Cryptogonimus chyli is a common parasite in the ceca and intestine of centrarchid fishes, particularly abundant in the rock bass, *Ambloplites rupestris*. Nothing is known of its life cycle except for a single encysted metacercaria found by Osborn (1910) in the membrane between the fin rays of a rock bass at Lake Chautauqua, N. Y., and figured by him. This metacercaria was considered to be that of *Cryptogonimus chyli* on the basis of its two suckers (acetabulum and gonotyl).

A few encysted metacercaria, which by their morphology seem undoubtedly to be immature specimens of this worm, were found in the flesh of *Perca flavescens*. Four were found in one fish, and one in each of several

others. The cysts measured 300 to 350μ in length and about 200 to 225μ in diameter, with a host cyst 45 to 60μ thick, whereas the single cyst figured by Osborn measured about 400 to 450μ, with no host cyst shown. The cyst is whitish in color, with no pigment cells around it. There is no space between the delicate transparent parasite cyst and the fibrous host cyst, and the parasite fills the inner cyst, in which it is bent approximately double on itself. The liberated parasite in relaxed condition measures about 400 to 500μ in length and 150 to 170μ in width. The cuticle in the anterior two-thirds of the body is spiny, and shows the typical dermal glands seen in the adult worms. The huge oral sucker varies from 125 by 125μ to 120 by 100μ. The pharynx, separated from the oral sucker by a prepharynx about equal to it in length, measures 52 to 45μ in length and 30 to 35μ in diameter. There are a pair of large black eyespots, 10μ in diameter, at either side of the pharynx. The ventral sucker and gonotyl are situated about 1/3 to 2/5 the length of the body from the anterior end. The gonotyl, 45 to 60μ in diameter, is slightly larger than the ventral sucker, which lies immediately behind it and at a deeper level, so that, as viewed from the ventral side in a relaxed specimen, the anterior half of the ventral sucker lies under the gonotyl. The Y-shaped excretory bladder is large and filled with refractile granules; the stem is about one-third the length of the body and the forks somewhat longer, ending at about the level of the pharynx. The testes are visible as two round bodies lying side by side about the middle of the length of the bladder stem. The ovary is very inconspicuous in living metacercariae, but appears as a small body about half the diameter of the testes, lying just anterior to the right testis, nearer the ventral surface.

The metacercarial cysts differ from those of the related *Caecincola parvulus* as described by Lundahl (1941) in having thicker and unpigmented host capsules and in the large size of the parasite cysts. The contained parasites, of course, show anatomical differences comparable with those of the adult worms.

Since *Cryptogonimus chyli* is a very abundant parasite in *Ambloplites rupestris* at Lake Itasca, it is doubtful, in view of the small number of cysts found, that the perch is the optimum host for these metacercariae.

APOPHALLUS sp.

A species of *Apophallus* closely resembling *A. imperator* was found quite commonly in the flesh. The cysts were surrounded by a sufficient accumulation of pigment cells to give a speckled appearance, but no dense coating of these cells, such as occur around *Neascus ambloplites*, were observed. The hard, glassy cysts of this species are quite unlike cysts hitherto described for members of this genus, and will be described elsewhere by Bruce Warren.

SUMMARY

Of eight species of metacercariae found in *Perca flavescens*, three species of *Neascus* are described as new, and a new *Apophallus* metacercaria is

reported. The metacercariae of *Cryptogonimus chyli* are reported from this host for the first time.

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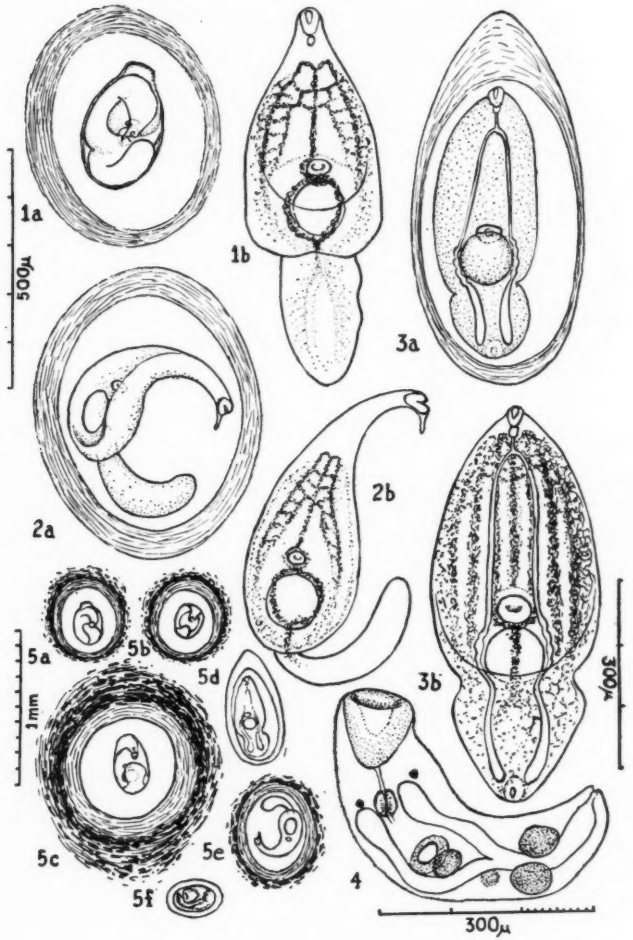

Figs. 1-5.—1. *Neascus pyriformis*. a. host cyst with enclosed parasite cyst and parasite. b. liberated parasite; 2. *Neascus longicollis*. a. host cyst, lined on inside by thin parasite cyst and free parasite inside, b. liberated parasite; 3. *Neascus ellipticus*. a. host cyst lined on inside by thin parasite cyst, and free parasite inside, b. liberated parasite; 4. *Cryptogonimus chyli* metacercaria freed from cyst; 5. Five species of metacercarial cysts drawn to scale. a. *Neascus pyriformis*, b. *N. bulboglossus*, c. *N. ambloplitis*, d. *N. ellipticus*, e. *longicollis*, f. *Cryptogonimus chyli*.

Scales: Upper left—figs. 1a, 2a, 3a; Lower right—figs. 1b, 2b, 3b; Lower left—figs.

Geographical Affinities of the Flora of North Dakota*

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Introduction

The state of North Dakota, like most political units, has political boundaries rather than geographic barriers to delimit its area. Plants, ignoring such divisions, continue their migrations until stopped by climatic extremes, unfavorable edaphic conditions or biotic interference.

In North Dakota some species may reach their northern limits because of temperature extremes, others their western limits because of precipitation deficiencies. Many species, moving eastward, are checked when they meet the competition of others more aggressive. Biotic interference has been especially severe since the plow of the white man broke the plains.

The available flora acted upon by physical and biotic factors has resulted in a prairie vegetation of short grass in the western part of the state, tall grass in the east, with a transition zone of mixed prairie lying between. Locally, edaphic conditions permit the occurrence of more mesic plants or restrict the vegetation to a few hardy desert species.

Acknowledgement

The writer wishes to thank Dr. E. Lucy Braun, under whose tutelage this study was begun, Dr. O. A. Stevens, who generously shared his extensive knowledge of North Dakota flora and made available manuscript and unpublished distribution data, Dr. Margaret Fulford and Dr. Lyman B. Smith for reading portions of this paper and offering helpful suggestions.

Physiography

North Dakota extends into two physiographic provinces (Fenneman, 1931, 1938), the Central Lowland and the Great Plains. The relief of the entire state is relatively low. The highest point is Black Butte, in Slope County, 3468 feet above sea level. The general elevation is approximately 3000 feet in the southwest corner of the state, sloping gradually to less than 800 feet in the northeast corner (fig. 1).

The two provinces are divided by a low indefinite east-facing escarpment, five to twenty miles wide, 300 to 600 feet high.

West of the line lies the Missouri Plateau section of the Great Plains province, which extends from the Pine Ridge escarpment in southern South Dakota northward to an undetermined boundary in Canada. It is a wide-

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spread rolling upland beveling Upper Cretaceous and Tertiary strata which apparently represent a once continuous surface from which newer and sharper relief has been carved. Along its eastern edge it is being consumed by the gradual westward spread of the Central Lowland.

A number of monadnocks, such as Sentinel Butte, Black Butte and others, rise to an almost uniform level 400 to 600 feet above the peneplain. These buttes are characteristically flat topped and protected by strong sandstone. Still higher beds once covered them and at least 1000 feet of rock were eroded away in forming the peneplain which surrounds them. A number of eminences, presumably identical in character, stand out on the plains of Montana, like giant stepping stones westward toward the Rocky Mountains.

"Badlands" are developing upstream along the Little Missouri River in southwestern North Dakota due to vigorous renewed erosion of the peneplain.

East of the boundary is the western Young Drift section of the Central Lowland province. The elevation is lower than west of the line due to the approximate completion of a more recent cycle of erosion. The gently rolling underlying rock surface is chiefly Cretaceous, overlain by relatively smooth glacial deposits, mostly ground moraine. Bedrock is exposed only occasionally where streams cut through the drift. About 25 miles from the eastern border of the state, the land levels off to the flat Red River Valley, once the bed of glacial Lake Agassiz.

Along the west edge of the Red River Valley at the International Boundary lie the Pembina Mountains. They comprise an escarpment ex-

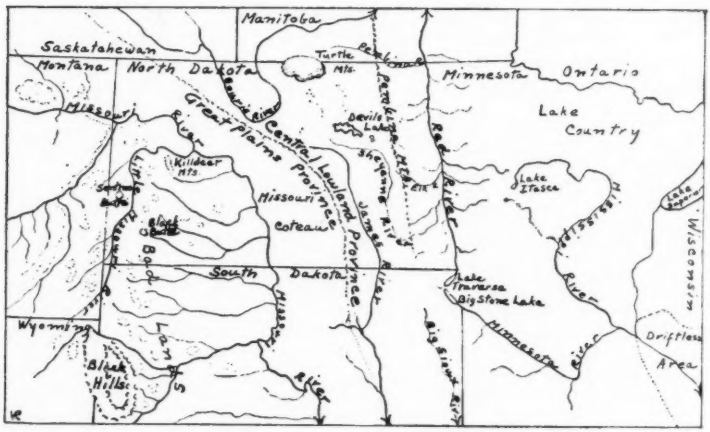

Fig. 1.—Physiographic map of North Dakota and adjacent areas.

posing outcrops of Upper Cretaceous chalk and shale, and rise 300 to 500 feet above the glacial filling of the valley. The elevation decreases southward and increases northward into Canada.

The Turtle Mountains are located at the point where the 100th meridian crosses the International Boundary. They cover an area of about 800 square miles and consist of hills, lakes and ponds. They are overlain by an estimated 100 feet of drift. The slopes are not steep but the highland is relatively prominent, rising 400 to 600 feet above the surrounding plain.

Glaciation occurred more than once in North Dakota. West and south of the Missouri River, in a belt about 25 miles wide, can be found remains of glacial drift of Iowan age. The deposit presumably was thin and the time since its deposition has been so long that an erosion topography has been fairly well reestablished.

The topographic effects of the most recent glaciation, the Late Wisconsin, are far more important, not only because of the larger amount of drift deposited but because of the recency of the event.

Like all previous glacial advances over North Dakota, its origin was at the Keewatin center, west of Hudson Bay, and it moved southward in lobes which intermittently progressed and regressed over the entire eastern part of the state. To the westward the ice mass climbed the escarpment of the Missouri Plateau, but having done so, lost its energy and was unable to proceed much farther. In successive small advances and retreats it built its reduplicated terminal moraines. In places, there remained several hundred feet of uneroded, stony glacial debris, on top of the plateau and in the valleys which formerly indented its slopes. This strip of moraine mantled plateau, 15 to 25 miles wide, bounded on the west by the Missouri River whose northward flow it deflected, overlooking the Central Lowland on the east, is known as the Missouri Coteau.

Eastward on the Lowland as far as the shoreline of glacial Lake Agassiz (fig. 2) the area is chiefly covered by ground moraine. The effect of glaciation was principally smoothing of the surface by abrading hills and filling valleys.

As the ice moved southward it effectively dammed northflowing river systems. Thus was formed Lake Agassiz, in the valleys of the present Red, Saskatchewan, and upper Nelson rivers, flooding an area of 110,000 square miles, which is greater than the combined areas of the present Great Lakes. Of that area, 6800 square miles is now North Dakota. Lake Agassiz was more than 400 feet deep at the International Boundary and rose to 650 feet higher than the present level of Lake Winnepeg, its remnant and successor.

Lake Agassiz overflowed at the lowest col in the divide between the basins of the present Red and Minnesota rivers. Its outlet, glacial River Warren, flowed to the Mississippi in a course now marked by Lake Traverse, Big Stone Lake and the Minnesota River. The large volume of

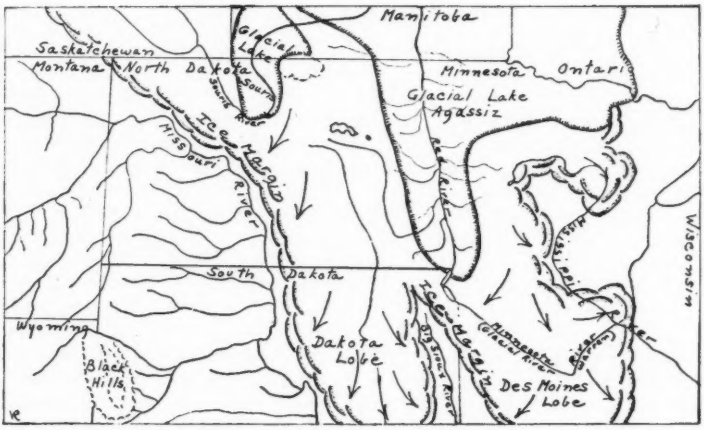

Fig. 2.—Map of North Dakota and adjacent areas showing maximum extent of late Wisconsin glaciation and location of glacial lakes Agassiz and Souris. In part after Leverett and Sardeson, 1932.

water it carried cut a trench 200 feet deep and one-half to four miles wide.

In the lake bed, a deep silt layer was deposited. Along the western shore where the Elk, Pembina and Sheyenne rivers entered the lake, sandy deltas developed and today remain as dune areas.

Ultimately the ice dam retreated northward and disappeared, revealing a sinking of the land. Drainage to Hudson Bay resumed.

Between the Turtle Mountains and the Missouri Plateau is the flat valley of the Souris River which enters the state southward from Saskatchewan, forms a loop and then flows northward into Manitoba. In glacial time this ponded to form Lake Souris.

Drainage of the glaciated portions of North Dakota is still young. Except near large rivers, streams are widely spaced. Few channels have been developed except along lines of depressions which were ready made when the ice vanished. Partly on account of the young drift topography and partly by reason of less rainfall, many small areas have only internal drainage. Brackish Devils Lake, formerly 40 miles long and draining into the Sheyenne River, is now the hydrographic center of an area of 3500 square miles.

Preglacial drainage of the Dakotas was apparently almost all northward. During glaciation all major streams were deflected southward because of ice dams and morainic barriers. Postglacial adjustments have permitted all except the Missouri River and its tributaries to resume approximately their original channels toward Hudson Bay.

PRESENT CLIMATE

North Dakota, situated at the geographic center of North America, is subject to a rigorous continental climate. With possible temperature extremes of —60°F. in winter and 120°F. in summer, and an annual average precipitation which some years may be as low as eight inches, the floristic population is restricted to hardy species with great resistance to climatic stress and those relicts or pioneers which are established in locally suitable edaphic areas.

Following the classification of Thornthwaite (1931), the temperature-efficiency rates as microthermal. The annual mean temperature for North Dakota ranges from about 36°F. to 44°F. (U.S.D.A. 1941). The average number of days a year when the temperature reaches 90°F. or higher is 14, and the average number with zero or lower is 53. The average growing season has about 121 days without severe frosts. However, killing frosts have occurred as late as the first part of June, and as early as the first days of September. The long duration of extreme weather and the short growing season undoubtedly prevents many species from becoming established.

On the basis of precipitation-effectiveness (Thornthwaite, 1931), the climate may be classified as subhumid in approximately the eastern third of the state and semiarid in the western two-thirds. Moisture is deficient at all seasons of the year. Annual precipitation averages 19.53 inches in the eastern part, 16.32 inches in the middle, and 15.38 inches in the west.

The boundary between the subhumid and semiarid prairie is transitional and variable. In the subhumid lands, one to ten years out of 20 are likely to be so deficient in rainfall as to be designated as dry or semiarid (U.S.D.A., 1941). The semiarid region has occasional humid years and not infrequent desert periods. The fickleness of precipitation is illustrated by data from Jamestown, N. D., near the western edge of the subhumid zone. In the course of 35 years, 15 years have been moist subhumid, 13 dry subhumid, five semiarid, one humid and one arid.

Such fickleness effects instability in the floristic pattern. In moist years, mesophytes make gains, only to be repulsed by a series of dry years and replaced by deeper rooted or otherwise better adapted xerophytic species.

SOILS

The soils which have developed as products of the subhumid to semiarid climate and prairie vegetation interacting on the parent material are predominantly Pedocals, lime accumulating soils (U.S.D.A., 1938).

The most striking are the Chernozems, black earths, which exhibit a darker surface layer than any other upland soils. They develop in temperate subhumid grasslands and are found in North Dakota on the glacial drift and lacustrine deposits of approximately the eastern third of the state.

In the western part of the state, where the climate is drier and the vegetation more sparse, Chestnut soils occur. They are less dark than the Chernozems and have developed on unglaciated sandstone and shale as well as on glacial drift.

In addition to the Pedocals, there are a few localized exceptions. Podzol has developed on the relatively small area of the Turtle Mountains, which are overlaid by poorly drained glacial drift supporting bog and forest vegetation. Dune sands occupy the Sheyenne River delta and similar deposits. The rough, broken lands of steeply eroded clays and soft shales along the Little Missouri River and the alluvial soils along the Missouri River are so recent that they are characteristic of the parent material, unchanged by environment.

Small areas, such as many of the lower buttes, are capped by scoria, a slag-like substance due to the partial fusion of clays by the natural burning of coal beds. The soil bordering many of the poorly drained lakes and ponds becomes excessively saline, especially in dry years. These are locally known as "alkali beds."

The exceptional areas are interesting floristically because they support the more unusual species, particularly the relicts.

VEGETATIONAL HISTORY

In the distant past the climate of North Dakota was much more clement than today and permitted a vegetation of luxuriant forest. Fossil records show that during Cretaceous and Early Tertiary time palms, *Metasequoia, Gingo, Cercidiphyllum, Fagus, Sassafras* and other associated warm temperate and subtropical mesophytes ranged well up into the area (R. W. Brown, 1949, personal communication).

Elevation of the western mountains, the Rockies and particularly the Cascades, begun at the close of the Cretaceous, continuing nearly to present height in Miocene, with a general regional uplift in Pliocene, induced drier mid-continent conditions by cutting off the inflow of humid air and precipitation from the Pacific Ocean. Gradually the great plains east of the Rockies became semiarid and forest land gave way to prairie (Schuchert and Dunbar, 1933).

With the onset of glaciation in Pleistocene time, the climate became cooler and more humid. And, as Sears states (1935), "the general theory is that tundra, scrub, conifers and deciduous forest shifted as belts before the advancing ice, then followed back in its wake as it melted." There is no evidence, however, to suggest that such succession occurred in North Dakota.

But, as Sears continues, "actually, of course, the ice extended into the interior grasslands as well as into the forest regions." Tyrrell (1910), referring to the grassland region of Canada just north of North Dakota, pointed out that the ice spread southward and later retired northward over plains and prairies and that "the whole known climatic history of these grassy plains is therefore included in the statement that a cold climate was succeeded by a dry continental climate, under neither of which conditions was a forest growth possible." Such was the case in North Dakota. The great plains then, as now, were in the rain shadow of the western mountains. For example, suggesting that at that period the vegetation, the cli-

mate, and edaphic conditions must have been essentially the same as at present, deposits of pre-Wisconsin Peorian interglacial age from Bronson, in northern Minnesota, about 25 miles east of the North Dakota line, have yielded plant materials, the majority of which are specifically the same as are found there today (Rosendahl, 1948).

The cool, humid periods of glacial advance, alternating with warm, drier interludes of retreat, resulted in successive destruction and reestablishment of vegetation. The most recent advance, the late Wisconsin, overwhelmed all of North and South Dakota east of the Missouri River, most of Minnesota, and extended southward over Iowa as far as Des Moines (fig. 2). The axis of glacial movement was from the Keewatin center southward along the Red River valley. At approximately the North-South Dakota border, the ice mass separated into two lobes, commonly referred to as the Dakota and the Des Moines. Ice free areas remained west of the Missouri River, south of the aforementioned lobes, with a wedge protruding northward between them in the present valley of the Big Sioux River, and in central Minnesota within about 75 miles of the North Dakota line (Leverett and Sardeson, 1932).

Presumably, the ice moved southward from a region of tundra and boreal conifer forest. Along its western flank it progressed across transition aspen woodland, into the prairie area of Canada and the Dakotas. Southeastward across Minnesota, conifer forest maintained a vanguard position and ultimately extended considerably beyond its present range.

As the encroaching ice obstructed the north flowing drainage systems, increased moisture due to ponding of streams must have permitted invasion of a few pioneer forest species. Aspen woods probably developed in mesic situations in North Dakota, with willow thickets and wet meadows occupying the lowlands and prairie remaining on the drier hilltops. Further stages in forest succession probably did not occur because cooling of the climate was causing temperate deciduous forest to migrate southward and the boreal conifer forest in Minnesota was unable to expand westward into North Dakota because of the ice barrier in the Red River valley.

Cooler conditions during glaciation also depressed montane vegetation to lower altitudes and Rocky Mountain flora, along with an intermingling of boreal species which were moving southward in the mountains, spread eastward onto the Black Hills and the Missouri Plateau section of western North and South Dakota. There are a number of such species persisting in that area today, apparently as relicts.

Finally, when the ice began to wane, its recession was back toward the Red River axis, with the final phase, or substage, of late Wisconsin represented by an ice lobe mainly in the Red River drainage basin. Melting of the southern tip of this lobe marked the preliminary stage of glacial Lake Agassiz. With continued northward melting of the ice, water ponded until it rose sufficiently to flow southward, as the glacial River Warren, to the Mississippi River.

On the basis of the rate of erosion of the Minnesota River valley by

the River Warren and the rate of recession of St. Anthony Falls at Minneapolis, Leverett has estimated the beginning of Lake Agassiz to have been about 18,000 years ago. Drainage southward is believed to have continued until about 9000 years ago at which time the ice had receded so far northward as to permit resumption of drainage northeastward to Hudson Bay.

This chronology would indicate that since glaciation there has been considerable time for reinvasion of vegetation into North Dakota, but somewhat less than has been available for migration into other states farther south and east. The turning point in glaciation, when the ice sheets began their last retreat from the upper Mississippi valley and southern New England is believed to have occurred some 25,000 or 30,000 years ago (Schuchert and Dunbar, 1933).

Because of widespread lake and swampland, hydrophytes were probably the first reentrants into North Dakota. There was doubtless an early return of willow, aspen, and birch. The onset of the postulated xerothermic period (Gleason, 1922, and others) would have favored return of prairie, the northeastward migration of southwest desert species, and a decline of the more mesic montane species.

Eastern deciduous forest migrated northward in the river valleys, especially along the Minnesota and the Big Sioux, up into southeastern North Dakota (fig. 3). The deep rooted, xeric bur oak, the quick growing boxelder, green ash, and American elm were among the vanguard and today have a wider distribution than the more requirant species such as basswood and hornbeam.

There is no evidence to suggest that North Dakota underwent any postglacial spruce to pine to deciduous forest succession as did the eastern states (Sears, 1948). Boreal conifers continue to be absent from the native vegetation although a number of their associates do occur. Some of the more mobile species, such as aspen and birch, apparently preceded the ice across the state and then followed it northward as it withdrew. Other northern or Canadian species, because of their limited distribution, so far as available records indicate, appear to have invaded North Dakota from the northeast relatively recently, perhaps only since the removal of the Lake Agassiz barrier.

Tundra has left no traces, if it ever existed in North Dakota. Rosendahl (1948), after examination of plant materials deposited "in the early stages of Lake Agassiz" at Moorhead, Minnesota, just across the line from North Dakota, states, "it is significant that none of the species found are tundra plants and there is no supporting evidence for assuming a tundra stage in the revegetation of the area." Rather, some 30 vascular species identified are "all characteristic components of the present day flora of the region."

PRESENT FLORA

The present flora of North Dakota includes about 900 native species (Stevens, 1922, 1950). Those of the prairie are predominant but also represented are many species whose affinities are with other formations, for-

est or desert, or are so widespread geographically as to be essentially cosmopolitan.*

Those well within their normal distribution, the intraneous species, comprise about 55 percent of the total flora. The remaining 45 percent, extraneous species, which are at or near the margin of their ranges, forms a slightly smaller group, of diverse origin and apparently restricted both by climate and physiographic history.

Introductions, which add roughly 150 species to the present flora, chiefly from Europe, are not considered in this paper.

The following outline presents the approximate percentage of species included in each of the various elements, broadly delimited, of the native flora of North Dakota.

I. Intraneous Flora	55
A. Widespread species	15
B. Prairie species	40
II. Extraneous Flora	45
A. Eastern deciduous forest species	20
B. Northern coniferous forest species	15
C. Rocky mountain species	5
D. Southwestern desert species	5

I. INTRANEOUS FLORA

A. WIDESPREAD SPECIES

Approximately 15 percent of the native flora of North Dakota is composed of widespread species. Many of these are transoceanic and range not only widely over North America but extend over other continents as well. Their occurrence in North Dakota is not unexpected. In most cases point of origin as well as lines of migration have become obscured. A number are aquatics, which find their localized habitats in any or all plant formations, forest, grassland or desert, and probably were among the early entrants into deglaciated territory.

Representative of the more or less cosmopolitan species found in North Dakota are: *Botrychium virginianum, Cystopteris fragilis, Pteridium aquilinum, Potamogeton pectinatus, Ruppia maritima, Zannichellia palustris, Phragmites communis, Cyperus esculentus, Lemna minor, L. trisulca, Spirodela polyrhiza, Juncus bufonius, Atriplex patula, Ceratophyllum demersum, Myosurus minimus, Centunculus minimus.*

Others, widespread around the northern hemisphere but not established on the southern continents, include: *Naias flexilis, Eleocharis acicularis,*

* Floristic data in this paper, including the distribution records in figures 3, 4, and 5, are supported by specimens in the herbarium of the North Dakota Agricultural College at Fargo and in the United States National Herbarium, Washington, D. C.

Ranunculus pensylvanicus, R. scleratus, Rorippa islandica, Humulus lupulus, Monotropa uniflora, Utricularia vulgaris.

A third group is found rather widely distributed over temperate North America, with many of the species ranging north to Alaska or south into Central America but not crossing to other continents. Among such are: *Sparganium eurycarpum, Potamogeton foliosus, Sagittaria latifolia, Sphenopholis intermedia, Scirpus validus, Heteranthera dubia, Juncus torreyi, J. nodosus, Corallorhiza maculata, Parietaria pennsylvanica, Urtica gracilis, Polygonum ramosissimum, Silene antirrhina, Geranium carolinianum, Rhus radicans, Heracleum lanatum, Sium suave, Verbena bracteosa, V. hastata, Ambrosia artemisiifolia.*

B. PRAIRIE SPECIES

Since North Dakota lies entirely within the grassland formation (Shantz and Zon, 1924), it is not surprising to find that a comparatively large portion of the flora, about 40 percent, is composed of prairie species. Climatic conditions over the state are most conducive to prairie development. Only the exceptional, localized situations favor maintenance of other types of vegetation.

The sub-humid eastern part of the state and a few moist valleys, or draws, farther west permit the development of tall grass prairie with *Andropogon furcatus, Sorghastrum nutans,* and *Stipa spartea* as dominants. Accompanying them are mid grasses such as *Andropogon scoparius, A. paucifloras, Bouteloua curtipendula, Elymus canadensis, E. glaucus, Koeleria cristata, Panicum virgatum, Sporobolus heterolepis* and numerous forbs including *Lilium umbellatum, Anemone cylindrica, Glycyrrhiza lepidotum, Linum sulcatum, Gentiana puberula, Lithospermum canescens, Gerardia aspera, Penstemon gracilis, Campanula rotundifolia, Aster laevis, Helianthus maximilliana, H. subrhomboideus, Kuhnia glutinosa, Liatris scariosa.* Actually, such communities have been much reduced by the encroachment of agriculture.

Over the western part of the state where arid conditions prevail, and eastward on dry slopes and overgrazed areas, short grass predominates. Most important is *Bouteloua gracilis,* with *Buchloë dactyloides, Agropyron smithii, Bouteloua hirsuta, Stipa comata, Carex filifolia, Allium reticulatum, Draba nemorosa, Psoralea argophylla, Linum rigidum, Sphaeralcea coccinia, Viola nuttallii, Gaura coccinia, Phlox hoodii, Collomia linearis, Plantago purshii* and other prairie species with relatively low moisture requirements.

Between these extreme prairie types lies the intermediate mixed prairie. This is characterized by the bunch habit of the dominants, *Andropogon scoparius, Bouteloua curtipendula,* and *Koeleria cristata.* Shorter grasses, particularly *Bouteloua gracilis,* and *Buchloë dactyloides,* occupy the interspaces. Other frequent species include *Festuca octoflora, Muhlenbergia racemosa, Panicum capillare, P. scribnerianum, P. virgatum, Sporobolus cryptandrus, Rumex mexicanus, Anemone cylindrica, Erigeron ramosus,* and *Solidago serotina.*

Here conditions in general are not sufficiently humid to permit the taller grasses to crowd out the xerophytic short grass species nor arid enough to eliminate the mesophytic grasses. A series of drought years, several successive humid years, or slight variations in elevation, exposure, soil texture, or grazing will considerably weight the floristic balance in favor of one group or the other. Studies by Weaver and his associates (1934, 1939), Hanson and Whitman (1938) and others have contributed greatly toward understanding of these interrelationships.

The mixed prairie species, both grasses and forbs, are sufficiently adaptable and so easily disseminated that they occur not only in more than one type of prairie in North Dakota but also in meadow, prarie, forest openings and disturbed areas almost throughout North America, lacking, in most cases, only in the high mountains of the west and in the southern Appalachians.

Geographically, the tall prairie species tend to show relationship to mesophytes of the humid east and the short grass to the xerophytes of the arid southwest. Some of the mid species are circumboreal components of montane and boreal meadows. However, the mobility of the species involved and the wide distribution apparently achieved during the postglacial xerothermic period somewhat obscures such affinities. Nevertheless, several major distribution patterns are evident in addition to the widespread range of the mixed prairie species.

The first group, comprising about one-fourth of the prairie species, has a range eastward from the Rocky Mountains, extending across the Mississippi River into the Prairie Peninsula of Illinois, Indiana, and Ohio. Included are: *Andropogon furcatus, Sorghastrum nutans, Stipa spartea, Astragalus plattensis, Dalea alopecuroides, Linum sulcatum, Asclepias syriaca, Gentiana puberula, Phlox pilosa, Lithospermum canescens, Houstonia longifolia, Helianthus rigidus, H. tuberosus, Solidago rigida.* Found in this group are the dominants of the tall grass prairie and many species of the mixed prairie.

A second pattern is shown by a group of species whose range extends from the Mississippi River westward into the intermontane prairies of the Rockies. About one-half of the total prairie species are included here. Mostly they are of the short grass plains, among them: *Agropyron hallii, A. smithii, Aristida longiseta, Bouteloua gracilis, Buchloë dactyloides, Allium reticulatum, Leucocrinum montanum, Comandra pallida, Rosa fendleri, R. woodsii, Lupinus argenteus, L. pusillus, Polygala alba, Sphaeralcea coccinea, Viola nuttallii, Gaura coccinea, Oenothera serrulata, Mentzelia decapetala, Penstemon angustifolium, Gilia minima, Solanum rostratum, Plantago purshii, Aster pauciflorus, Cirsium megacephalum, Helianthus annua, H. maximilliana, H. petiolaris, Liatris punctata, Ratibida annua, H. maximilliani, H. petiolaris, Liatris punctata, Ratibida columnaris.* In a few cases, especially among the short grasses, the easternmost stations of this group may be recent introductions.

A third group, comprising most of the remaining 25 percent of the prairie flora, are more or less limited to the strip of states lying between the Mississippi River and the Rockies. Mostly these species are found in sandy areas. A few such are: *Petalostemon villosum, Psoralea argophylla, P. esculenta, Linum rigidum, Euphorbia geyeri, E. marginata, E. missurica* var. *intermedia, Eriogonum annum, Oenothera caespitosa, Penstemon gracilis, P. grandiflorus, Plantago spinulosa, Brauneria angustifolia, Senecio plattensis, Solidago mollis.*

A few prairie species are restricted in range to the north central states, roughly the area between the Mississippi River and the Rocky Mountains, from Kansas northward. This may be because the species are younger or, in some cases, at least, because narrower specific limits have been applied. A few examples of this group are: *Calamagrostis montanensis, Carex assiniboinensis, Lesquerella arenosa, Rosa arkansana, Astragalus bisulcatus, A. flexuosus, Phlox hoodii, P. andicola, Lygodesmia rostrata.*

The amount of endemism in North Dakota is uncertain. A number of new species have been described from the region but almost all have been reduced to synonymy, usually, for being merely environmentally induced variations.

II. EXTRANEOUS FLORA

The 45 percent of the flora classified as extraneous to North Dakota includes those species which are at the edges of their ranges and are, in fact, beyond the margins of the formations to which they belong. In general, they are either more mesic or more xeric than the prairie species. Those advancing from the west are checked when they meet and fail to withstand the competition of the eastern species. The mesic eastern species are as effectively eliminated where they encounter the unfavorable conditions that only xerophytes can withstand.

A. EASTERN DECIDUOUS FOREST SPECIES

Forest, in North Dakota, occurs almost exclusively in the Turtle, Pembina, and Killdeer Mountains and as narrow strips, a few hundred feet wide, along the larger streams.

Of the eastern deciduous forest dominants, which northwestward diminish to maple-basswood climax (Braun, 1947), only basswood (*Tilia americana*) reaches North Dakota. The sugar maple (*Acer saccharophorum*) disappears about 50 miles east of the North Dakota-Minnesota line. There was an early collection at Rutland, Sargent county, in the southeastern part of the state, reputedly from two native trees, which, however, have never been relocated. A few cultivated specimens occur in Fargo but their growth seems retarded.

In spite of the relatively small area suitable for the eastern mesophytes, they constitute about 20 percent of the total native species of North Dakota. The largest number are found along the Red River and a few miles to the west where they probably became established at the margin of

glacial Lake Agassiz. They apparently arrived via the Warren-Minnesota River valley and the Big Sioux River system of eastern South Dakota (fig. 3). In the group so limited are, for example: *Onoclea sensibilis, Allium tricoccum, Smilacina racemosa, Trillium cernuum, Arisaema triphyllum, Pilea pumila, Anemone quinquefolia, Clematis virginiana, Dicentra cucullaria, Penthorum sedioides, Ribes cynosbati, Crataegus mollis, Desmodium acuminatum, Xanthoxylum americanum, Impatiens pallida, Orobanche uniflora, Veronica virginica, Eupatorium rugosum, Cirsium altissimum. Ulmus fulva* is grown as a shade tree but its native occurrence has not been verified.

An additional number of eastern mesophytes occur not only in the Red River valley but also a little farther west along the James River and in the Devils Lake region. Among these are: *Uvularia grandiflora, Hypoxis hirsuta, Ostrya virginiana, Laportea canadensis, Menispermum canadense, Ribes missouriensis, Geum canadense, Rhus glabra, Tilia americana, Gentiana andrewsii, Verbena urticaefolia, Mimulus ringens.*

While none of the preceding species has been found in the Turtle Mountains, the following have reached their present western limits in that area: *Festuca obtusa, Hystrix patula, Corylus americana, Sanguinaria canadensis, Impatiens biflora, Stachys aspera, Gerardia tenuifolia, Prenanthes alba, Rudbeckia laciniata.*

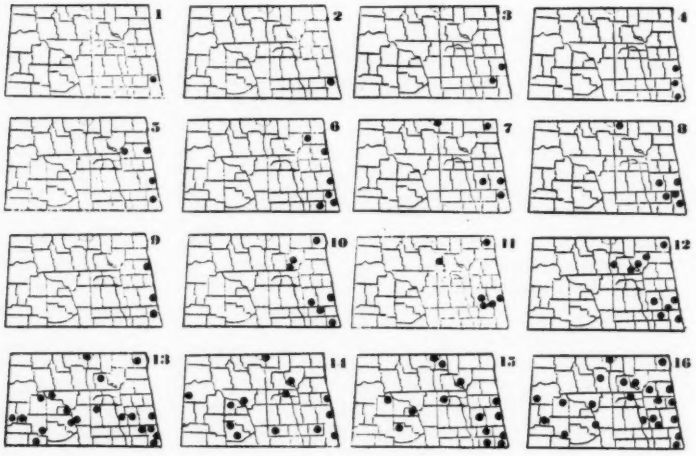

Fig. 3.—Eastern deciduous forest species in North Dakota, at or near their northwestern limits of distribution. (1) *Onoclea sensibilis.* (2) *Ribes cynosbati.* (3) *Allium tricoccum.* (4) *Eupatorium rugosum.* (5) *Caulophyllum thalictroides.* (6) *Arisaema triphyllum.* (7) *Hystrix patula.* (8) *Sanguinaria canadensis.* (9) *Xanthoxylum americanum.* (10) *Rhus glabra.* (11) *Ostrya virginiana.* (12) *Tilia americana.* (13) *Quercus macrocarpa.* (14) *Ulmus americana.* (15) *Prunus americana.* (16) *Ribes americanum.*

Some of the eastern species, better adapted to withstand drought, range across the Missouri River to western North Dakota and into eastern Montana. These include: *Polygonatum commutatum, Ulmus americana, Celtis occidentalis, Quercus macrocarpa, Polygonum scandens, Anemone virginiana, Ribes americanum, Fragaria virginiana, Prunus americana, P. pensylvanica, Amphicarpa bracteata, Desmodium canadensis, Lathyrus venosus, Celastrus scandens, Acer negundo, Vitis vulpina, Fraxinus pennsylvanica* var. *lanceolata, Monarda fistulosa, Viburnum lentago, Lactuca canadensis.*

About one-fourth of the eastern deciduous forest species in North Dakota are of Canadian-Alleghenian origin, including such examples as: *Anacharis planchoni, Scirpus fluviatilis, Juncus brachycephalus, Cypripedium candidum, C. reginae, Salix discolor, S. serrissima, Asarum canadense, Anemone canadensis, A. hudsoniana, Caulophyllum thalictroides, Viola pubescens, Hydrophyllum virginicum, Fraxinus nigra, Mentha canadensis, Pedicularis lanceolata, Scrophularia lanceolata.*

Their ranges, like those of the foregoing, vary somewhat in westward extension depending on their moisture requirements as well as rate of migration (fig. 3).

Absent from North Dakota, although found no more than 50 miles to the east in Minnesota are, in addition to *Acer saccharophorum,* such species as *Taxus canadensis, Populus grandidentata, Carpinus caroliniana, Ulmus thomasi, Quercus borealis, Hepatica americana,* and *Dirca palustris.*

B. Northern Coniferous Forest Species

Northern conifer forest is lacking from North Dakota. None of the boreal coniferous trees, *Abies balsama, Picea glauca, P. mariana, Larix laricina, Pinus banksiana, P. resinosa,* or *P. strobus,* are found native in the state although within about 50 miles east and northeast they are important in the vegetation of Minnesota and Canada.

Nevertheless, many associated species are present, composing about 15 percent of the total North Dakota flora. As mentioned earlier in this paper, there evidently was no migration of tundra or conifer forest across the state either before, or after, the late Wisconsin glacial advance. However, modification of the prairie region by increased humidity and soil moisture as the ice began to move southward must have favored some forest development. Aspen-birch woods probably became rather widespread but further stages in forest succession did not occur because the cooling climate was not conducive to temperate forest expansion northward and boreal conifer migration into North Dakota was cut off by the ice barrier. The aspen-birch woods persisted for some time, representing a subclimax to a boreal conifer forest climax which failed to materialize.

Subsequent xerothermic climate influenced the disappearance of boreal species. Only those in protected areas such as moist shaded locations in the Turtle, Pembina, and Killdeer Mountains and in spring-fed depressions in sand hills of the Sheyenne delta were able to persist, as relicts (fig. 4).

More recently, westward migrating species of the eastern deciduous forest have found suitable habitats in the same locations so that the resulting vegetation is an intermingling of mesophytes of diverse geographic origin.

The trees of the boreal forest which do range into North Dakota are: *Populus tacamahaca, P. tremuloides,* and *Betula papyrifera.* As understory or as dominants in treeless situations are various shrubs, such as: *Salix bebbiana, S. candida, Betula glandulosa, Ribes triste, Amelanchier alnifolia, Elaeagnus argentea, Shepherdia canadensis,* and *Cornus stolonifera.* Among the boreal semi-shrub and herbaceous plants have been found: *Carex aurea, Arabis holboellii, Drosera rotundifolia, Parnassia palustris, Potentilla fruticosa, Rubus pubescens, Viola rugulosa, Epilobium angustifolium, Cornus canadensis, Pyrola asarifolia, P. secunda, Arctostaphylos uva-ursi, Menyanthes trifoliata, Linnaea borealis,* and *Petasites sagittata.*

C. Rocky Mountain Species

Rocky Mountain species, which comprise about five percent of the North Dakota flora, are principally found in the unglaciated southwestern part of the state (fig. 5). The presence of some may be the result of recent migration. The majority probably are relicts of former more extensive communities. The monadonocks on which these species are chiefly found are themselves relicts, left behind in the westward retreat of the old Tertiary upland. As erosion has progressed, the upland has diminished to a few rocky buttes and dissected bad lands. The developing peneplain, the ultimate product of this erosion cycle, provides a new and favorable habitat for prairie species, which soon acquire dominance.

During glacial periods, because of the prevailing cool, moist climate,

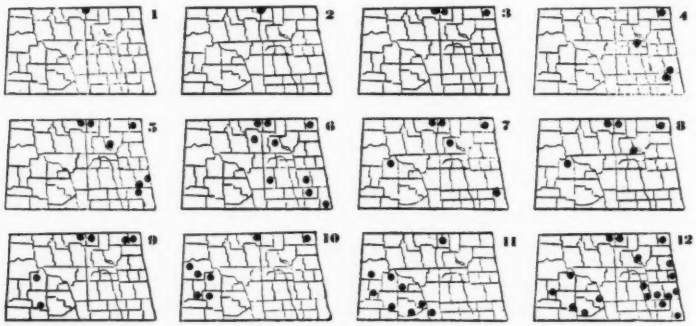

Fig. 4.—Northern coniferous forest species in North Dakota. Most also occur, as relicts, in South Dakota. (1) *Drosera rotundifolia.* (2) *Linnaea borealis.* (3) *Cornus canadensis.* (4) *Betula glandulosa.* (5) *Rubus pubescens.* (6) *Parnassia palustris.* (7) *Betula papyrifera.* (8) *Pyrola asarifolia.* (9) *Elaeagnus canadensis.* (10) *Arctostaphylos uva-ursi.* (11) *Arabis holboellii.* (12) *Viola rugulosa.*

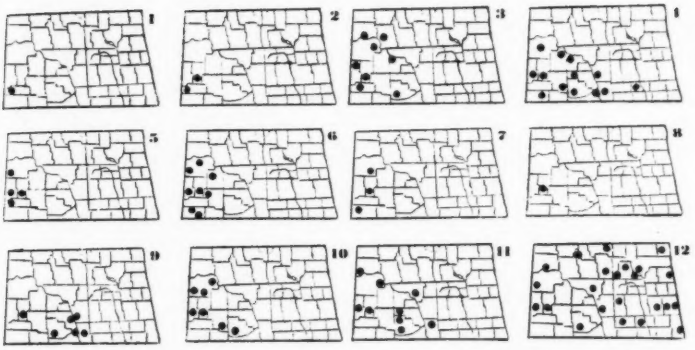

Fig. 5.—Rocky Mountain species. (1) *Pinus flexilis*. (2) *Pinus ponderosa* var. *scopulorum*. (3) *Juniperus scopulorum*. (4) *Rhus trilobata*. (5) *Calochortus nuttallii*. (6) *Lesquerella alpina*. Southwestern desert species. (7) *Artemisia tridentata*. (8) *Atriplex confertifolia*. (9) *Yucca glauca*. (10) *Sarcobatus vermiculatus*. (11) *Eurotia lanata*. (12) *Suaeda depressa*.

montane and alpine vegetation zones were depressed and there probably was considerable migration of Rocky Mountain species into western North Dakota. But in this case, as with the boreal flora, the increase of aridity, during and following deglaciation, would have been responsible for the decline of such vegetation and the increase of prairie and desert species. Only in a few localities, on buttes and in cañons of the badlands have a limited number of montane species been able to survive the climate and competition.

Most striking are three conifers, *Pinus flexilis*, *P. ponderosa* var. *scopulorum*, and *Juniperus scopulorum*. Other characteristic, though less conspicuous, species are: *Calochortus nuttallii*, *Disporum trachycarpum*, *Delphinium bicolor*, *Ranunculus glaberrimus* var. *ellipticus*, *Lesquerella alpina*, *Hedysarum cinerascens*, *Rhus trilobata*, *Androsace septentrionalis* var. *puberulenta*, *Gilia congesta*, and *Lappula texana* var. *columbiana*.

D. Southwestern Desert Species

Another five percent of the North Dakota flora is made up of migrants from the deserts of southwestern United States. Locally, they may be observed to dominate sizeable areas. Dry hillsides are studded with cactus, flats along streams may appear silvery with sagebrush, and saline spots, the "alkali beds," are populated almost entirely by halophytes from the Great Basin region.

In general, these species, although not restricted to the western part of the state, are most abundant there (fig. 5). Dry years tend to favor their eastward extension by reducing their competitors, principally the grasses.

Atriplex confertifolia and *Artemisia tridentata*, dominants in the Great Basin Desert (Shreve, 1942), occur in North Dakota but only in the western part of the state. Much more abundant are other species of these two genera, viz. the saltbushes, *Atriplex argentea, A. dioica, A. hastata,* and *A. nuttallii* and other sagebrushes, *Artemisia cana, A. dracunculoides, A. frigida, A. glauca, A. gnaphalodes,* and *A. longifolia.*

Additional species whose affinities are with the southwest deserts or have, since glaciation, reinvaded North Dakota from such areas are *Yucca glauca, Franseria acanthicarpa, Mamillaria missouriensis, M. vivipara,* and *Opuntia fragilis,* all of which occur on dry sandy or gravelly soils, and the halophytes, *Distichlis stricta, Eurotia lanata, Monolepis nuttalliana, Sarcobatus vermiculatus, Salicornia rubra, Suaeda depressa,* and *Allocarya californica,* which are found in and about the numerous saline areas of the state.

E. Coastal Plain Species

With the exception of *Juncus balticus* var. *littoralis,* none of Peattie's list of Atlantic coastal plain plants in the flora of the Great Lakes (Peattie, 1922) has been found to occur in North Dakota. "True" *Polygonum pennsylvanicum* L. may possibly be present but all collections, to date, have been identified as var. *laevigatum.*

In Minnesota, however, a third or more of the listed species have been found, on sandstone, in sand dune areas near Minneapolis, along the Minnesota River as far as Mankato, and up the Mississippi, some as far as its source at Lake Itasca, only about 75 miles east of North Dakota. Westward, in the Lake Agassiz bed and beyond, the calcareous nature of the soil may be a limiting factor in the distribution of coastal plain flora, but, presumably, migration is in progress and will proceed northward and westward where suitable habitats are available.

Summary

The vegetation of North Dakota is a part of the North American grassland formation, reflecting the influence of climate, physiographic history, and biotic factors upon the available flora. In localized areas, edaphic conditions permit the occurrence of more mesic plants or restrict the vegetation to a few hardy xeric species.

Approximately 55 percent of the flora is intraneous, of which 40 percent comprises prairie species and 15 percent species of widespread distribution.

The remaining 45 percent is composed of extraneous species: 20 percent are immigrants from the eastern deciduous forest; 15 percent are relicts of the northern coniferous forest; and five percent, each, are from the Rocky Mountains and from the deserts of southwestern United States.

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New Combinations in Salix (Sections Pellitae and Phylicifoliae)

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Many taxonomic papers create new species or raise varieties to specific rank. This paper reduces three species to varietal status, and two others to synonymy.

A. Salix Drummondiana Barratt and Its Western Relatives

In Section *Pellitae*, five species of *Salix* from the western part of North America have been named. Of these, only *S. Drummondiana* Barratt is here recognized as a species. Two others, *S. bella* Piper and *S. subcoerulea Piper*, are reduced to varietal rank. The final two, *S. Covillei* Eastwood and *S. pachnophora* Rydberg, are regarded as synonyms of *S. subcoerulea*.

Section *Pellitae*, in western North America, is composed of shrubs 1-4.5 meters tall; twigs and buds mostly glabrous and often thinly to densely pruinose; leaves subentire, silvery-tomentose beneath, with veins impressed above; aments precocious to subcoetaneous, sessile to subsessile; scales elliptic-oval to ovate, mostly acutish, black, long-villous; stamens 2, filaments free, glabrous; capsules 4-6 mm. long, sericeous; pedicels 0.5-1.5 mm. long, puberulent; styles 0.7-1.2 mm. long, mostly entire, puberulent at base; stigmas about half as long, entire to notched or divided.

In general, *S. Drummondiana* has non-pruinose subshining twigs, with short and broad leaves densely tomentose beneath; variety *bella* has twigs varying from non-pruinose to pruinose, and long narrow elliptical leaves with similar tomentum; while variety *subcoerulea* has twigs mostly densely pruinose, and oblanceolate leaves with shorter and less dense tomentum. Unfortunately, there are some wide variations from these standards, as discussed later.

The two representatives in northeastern North America, *S. pellita* Andersson and *S. argyrocarpa* Andersson, vary somewhat from the western group. The leaves often tend to become glabrate in age, and *S. argyrocarpa* is smaller in most characters, especially height, and leaf and capsule size.

1. Salix Drummondiana Barratt—Drummond Willow

Salix Drummondiana Barratt in Hooker, Fl. Bor.-Amer. 2: 144. 1838; Andersson (Nord Amerika Pilarter), in Öfvers. Kon. Vet.-Akad. Förhandl. 15: 123. 1858 (printed simultaneously, as Salices Boreali-Americanae, in Proc. Amer. Acad. Arts and Sci. 4: 63. 1868; Bailey and Bailey (Woody Pl. West. Nat'l. Parks), in Amer. Midl. Nat. Monogr. Akad. Handl. 6: 137-138. 1867 (in 1868, Andersson cites a "fig. 71" for this species in his Monog Salic., but none was published therein; Andersson in DC., Prodr. 16(2): 243. 1868; Bailey and Bailey (Woody Pl. West. Nat'l. Parks), in Amer. Midl. Nat. Monogr. 4: 42, 53-54. 1949; Ball in Standley (Fl. Glacier Natl. Park), in Contrib. U. S. Natl.

Herb. 22: 320, 323. 1921; Ball in Abrams, Illus. Fl. Pacific States 1: 503, fig. 1224. 1923; Henry, Fl. So. Brit. Col. 99. 1915; Macoun, J., Cat. Can. Pl. 1(3): 448. 1885; Rydberg, Fl. Rocky Mtns. and Adjac. Plains 196. 1917; Ulke (Fl. Yoho Park, B. C.) in Contrib. Biol. Lab. Cath. Univ. Amer. 14: 65. 1934.

S. pellita (in part) as determined by Ball for Farr (her No. 922, Laughing Falls, Yoho, in Contrib. Cat. Fl. Can. Rocky Mtns. and Selkirk Range), in Contrib. Bot. Lab. Univ. Penn. (3(1): 31. 1907, not Andersson.

S. sitchensis (in part) as understood by some northwestern authors, not Sanson.

S. subcoerulea (in part) as understood by some northwestern authors, not Piper.

Shrub 1-3 or 4.5 m. tall; twigs relatively short, stoutish, and divaricate, the younger yellowish-brown, pubescent to puberulent, older dark-brown to purplish-brown, subshining to shining, mostly glabrous; buds 3-7 or 10 mm. long, colored and clothed as the twigs; stipules on fruiting twigs none or minute, on summer foliage twigs sometimes 5-9 mm. long, obliquely lanceolate to obliquely semi-ovate, colored and clothed as the leaves; petioles 5-10 mm. long, colored and clothed as the twigs; blades narrowly to broadly elliptic-lanceolate, or narrowly to broadly oval, or oval-obovate (oblanceolate while opening), 3-7 or 10 cm. long, 1-3 or 4 cm. wide, or to 11-13 by 3-5 cm. on vigorous summer shoots, obtusish to apiculate or acute at apex, acutish to obtuse at base (acute while expanding), somewhat revolute at margin and entire or rarely micro-serrulate, dark green with impressed veins and pubescent or puberulent above, densely silvery-tomentose with secondary veins almost hidden beneath; midrib densely pubescent beneath, becoming glabrescent to glabrous and then yellow in age.

Aments precocious to subcoetaneous, sessile to becoming subsessile and bracted at base, 1-5 or 6 5 cm. long, 1-1.5 cm. wide, rather dense; peduncles 3-7 or rarely 10-12 mm. long, with mostly tiny bracts but rarely tiny leaves to 1-1.5 cm. long; scales elliptic-oval or ovate, mostly acutish when fully developed, 1-1.5 or 2 mm. long, black, long-villous, persistent; stamens 2, filaments free, glabrous; capsules 4.5-5.5 or 6 mm. long, subovate or pyriform, silvery-pubescent; pedicels 0.5-1 or 1.5 mm. long, stoutish, silky-puberulent; styles mostly 0.8-1.2 mm. long, often slow in elongating, usually entire, puberulent on basal portion; stigmas shorter, 0.3-0.6 mm. long, entire, notched, or divided; gland short, about as long as the stigmas.

Moist locations in mountain areas, at altitudes of 3000-7500 feet, from northwestern Montana, northern Idaho, and eastern Washington (Spokane Co.) northward to central Alberta and British Columbia. Flowers in May and June, fruit and opening leaves in June and July, varying with altitude.

Specimens of *S. Drummondiana* should be readily distinguished from those of all other members of section *Pellitae* by the usually broadly elliptic-lanceolate to broadly oval leaves, acute to obtusish at apex. Under two sets of conditions, however, these differences do not fully appear. The first relates to seasonal development. If specimens are collected when a plant is in flower, the leaves are just beginning to open, as in most precocious species. If collected when in fruit, the leaves usually are not yet fully expanded and often are still oblanceolate because the apical portion broadens first and the basal portion last. At this stage they may strongly resemble those of variety

subcoerulea, although generally with more dense tomentum. Most of Stanley's specimens from Glacier National Park were collected in these stages and were then (1919) determined by the writer as *S. subcoerulea*.

The second set relates to fragmentary material. A single herbarium specimen of most willows is but a fragment and seldom gives a picture of the characters found on the whole plant. Willows are especially variable and the leaves on an early twig may be very different from those on a late twig of the same plant (Ball, in Journ. Arnold Arb. 27: 371-385. 1946). As wide or wider differences occur in leaves from different plants of the same species. If a species, as *S. Drummondiana*, has relatively broad leaves and a variety, as variety *bella*, has longer and relatively narrower leaves, herbarium specimens almost inevitably will be found with leaves almost exactly intermediate between the two, although the leaves on the two plants as a whole might be distinctly different. If such a specimen has the twigs non-pruinose, it probably would be assigned to the species; if pruinose, then to the variety. Worse still, however, is a specimen consisting of a branching shoot with the narrowly elliptical leaves of variety *bella* on most twigs but the broadly elliptic-oval leaves of the species on one still-attached twig, as in Christ 17984 from Bonner County, Idaho.

The specimens cited below, probably representing the total range of the species, are located in the following designated herbariums: Carleton R. Ball (CRB), Catholic University of America (CUA), U. S. Forest Service (FS), U. S. National Herbarium (USN), and Washington State College (WSC). Many others have been determined by the writer but only those studied recently are cited. In general, locations are given from south to north.

MONTANA. Glacier National Park: *Vernon Bailey* on Aug. 29, 1917 (USN, as *S. sitchensis*); *A. S. Hitchcock* 11921 in 1914 (USN); alt. 7600 ft., *C. L. Hitchcock* 1942 in 1933 (CRB); *Bassett Maguire* 683, 684 in 1932 (CRB); *Maguire et al.* 5271, 5274. 5279, 5286, 5287 in 1934 (all CRB); *Paul C. Standley* 14915, 15224 15227, 15399, 15426 (CRB), 15432, 15758, 15894, 16742, 16762, 16781, 17130 (CRB), 17206, 17306, 17570 17820 (CRB), 18193, 18504, 18683, 18797 (all USN). COUNTY UNKNOWN (probably Flathead Co. or nearby): McDougal Peak, alt. 6000 ft., Flathead Lake, *Marcus E. Jones* on July 31, 1908 (USN, 2 sheets as *S. pellita*); Midvale, *L. M. Umbach* 310 in 1903 (USN).

IDAHO. KOOTENAI CO.: Honeysuckle Ranger Station, alt. 3000 ft., *Wilfred W. White* 22 in 1934 (FS 71189). BONNER CO. (all Priest Lake area): South end of Chase Lake at Lost Creek, south of Coolin, *J. H. Christ* 17956, 17958, 17960 in 1948 (CRB); Upper Priest Lake at outlet into Thorofare, *Christ* 18021, 18025 in 1948 (CRB); Priest Lake at mouth of Granite Creek, *Christ* 18027 18029 in 1948 (CRB); Priest Lake, C. V. Piper 11 on Aug. 28, 1916 (CRB, WSC); Coolin, foot of Priest Lake, *Piper* 6627 in 1923 CRB, WSC); Byers Hotel, head of Priest Lake, *Piper* 6643 in 1923 (CRB, WSC).

WASHINGTON. SPOKANE CO.: Spokane, *Piper* 3517 on Oct. 1, 1900 (CRB).

ALBERTA. Cypress Hills (extreme SE. corner of Province), *Robert C. H. Cormack* 7 in 1945 (CRB); Waterton Lakes Park: *M. O. Malte and W. R. Watson* 116740 (167), 116742 (169), 116743 (170), 116744 (171), 116754 (252), 116755 (253), 116756 (254), 116757 (255), 116760 (258), 116762 (339), 116763 (340), 116765 (342) all in 1925, at altitudes of 4200-4600 ft. or one at 5000 ft. (all CRB); *W. C. McCalla* 6556 in 1941 (CRB) and 6886 in 1942 (CRB); *E. H. Moss* 964 in 1940

(CRB). Southwest of Pincher Creek, *Moss* 1178 in 1941 (CRB). Crows-nest Pass area: *John Macoun* 94323 (6) in 1897 (CRB); *McCalla* 6832 in 1942 (CRB). Palliser Pass, alt. 7000 ft., *N. B. Sanson* 500 in 1922 (CRB. alpine depauperate). Rocky Mountains National Park (Banff and Vicinity): Cascade Creek, alt. 4650 ft., *McCalla* 2247 in 1899 (USN); *Sanson* 0109 in 1902 (CRB); *Sanson* 2, 46, 51, 147, 157, 240, 252, 253, 314, 2046, 2071, 2072, 2076, 2119, 2127, 2128, 2192 all in 1911 (all CRB); *Sanson* on Aug. 12, 1912 (CRB); 17 mi. se. of Banff, *Sanson* 104 in 1926 (CRB); 114, 116 in 1928 (CRB). Laggan, *J. Macoun* 68891 in 1904 (CRB); *Malte* 15 on July 11, 1913 (CRB). Lake Louise, *Malte and Watson* 116825 (1095), elev 5700 ft., in 1925 (CRB); *J. G. Jack* 2912 in 1922 (CRB). Clearwater River, northern boundary of Banff Park, *I. McTaggart Cowan* 5 in 1943. Jasper National Park: *W. P. Fraser* 14 in 1940 (CRB); *James M. Macoun* 95387 ni 1917 as *S. candida* (CRB); *McCalla* 7111, 7112 in 1942 (CRB); *Moss* 4712, 4713 in 1939, at alt. 5900 ft. (CRB).

BRITISH COLUMBIA. Kootenay Park: through *G. A. Hardy*, 10 in 1943 (CRB); *Sanson* in 1940 (CRB). Crows-Nest Pass: *Thos. T. McCabe* 6492, (15 ft. tall) in 1938 (CRB). Yoho National Park: *Edith M. Farr* 922 in 1905 (CRB, det. as *S. pellita*); 25 miles east of Golden, *McCabe* 6304 in 1938 (CRB); *Sanson* 818 in 1921 (CRB); Burgess Pass Trail, alt. 6500 ft., *Titus Ulke* 1125 on July 28, 1922 (CUA, very depauperate); alt. 7500 ft., *Ulke* on July 23, 1927 (CRB). Kicking Horse Pass, east of Field, *McCalla* 7447, in 1943 (CRB). Clearwater River Road, 20 miles from North Thompson River Road (approx. 52° N., 120° W.), *McCabe* 1047, 1048, 1051, 1052 in 1934 (CRB). Between Stanley and Barkerville (approx. 53° N., 121° W.), *McCabe* 955, 1082, 1089 in 1934 (CRB). 29 miles north of Prince George (approx. 54° 20′ N., 122° 40′ W.), *McCabe* 6946 in 1939 (CRB). The McCabe specimens presumably all are in the herbarium of the University of California also.

It should have been stated earlier that many of the specimens cited under *S. Drummondiana* and each of its two varieties, *bella* and *subcoerulea*, may have been distributed under a different one of these three names than that under which it appears here. Some northern specimens of variety *subcoerulea* have been distributed also as *S. pachnophora* and some California specimens as *S. Covillei*. Mention of this was made in the discussion of the Glacier Park specimens of the species. Only where specimens have been distributed under names not treated in this paper, as *S. candida, S. pellita,* etc., is that name inserted after the herbarium abbreviation.

2. **S. Drummondiana** Barratt, variety **bella** (Piper) n. comb.

Salix bella Piper in Bull. Torrey Bot. Club 27: 399. 1900; Bailey and Bailey (Woody Plants Western Natl. Parks), Amer. Midl. Nat. Monogr. 4: 53. 1949; Ball in Abrams, Illus. Fl. Pacific States 1: 503, fig. 1223. 1923; Piper and Beattie, Fl. SE. Washington and Adjac. Idaho 75. 1914; Rydberg, Fl. Rocky Mtns. and Adjac. Plains 196. 1917; Van Dersal (Native Woody Pl. U. S.), in U. S. Dept. Agric., Misc. Publ. 303: 245. 1938.

Twigs mostly longer, less puberulent and less shining, sometimes somewhat purplish, and, with the buds, often more or less pruinose; leaves narrower, oblong-lanceolate or narrowly elliptic-lanceolate, (or somewhat oblanceolate while unfolding), 4-8 cm. long, 1-2 cm. wide, or to 12 by 3 cm. on vigorous shoots, acute at apex, sometimes rounded at base, often less puberulent above, and the midrib beneath often becoming glabrate and yellowish earlier; styles averaging longer, to a maximum of 1.5 mm. long.

Variety *bella* ranges slightly farther south than the species, with sporadic occurrences in Valley County, Idaho, and northeastern Oregon. Northward

it reaches central Alberta but only southeastern British Columbia, and is less common in both. Flowering and fruiting occur as in the species. All specimens restudied recently by the writer are cited below. Herbarium abbreviations are the same as for the species.

MONTANA. LAKE CO.: Swan Lake, alt. 3000 ft., *M. E. Jones* on Aug. 24, 1908 (USN, 2 sheets, as *S. candida*, one annotated: "This is *Jones* 9138 in Herb. Mo. Bot Gard.") Glacier National Park: *Bassett Maguire et al.* 5272, 5273, 5276, 5277 in 1934 (all CRB); *Paul C. Standley* 18432 (USN; 18804 in 1919 (CRB). MISSOULA CO.: Flathead Forest, London Ranger Station, *W. W. White* 272, 273 in 1937 (FS 81719, 81720).

IDAHO. VALLEY CO.: Lake Fork, near McCall, alt. approx. 3500 ft., *J. H. Christ* 9616, 9629 in 1938 (CRB). CLEARWATER OR SHOSHONE CO.: Oxford Ranger Station, alt. 5000 ft., Clearwater Forest, *Epling and Houck* 9675, 9677 in 1926 (CRB). SHOSHONE CO.: North Fork of Clearwater River, *Christ, Gail, and Ward* 8757 in 1937 (CRB, 2 sheets); Clarkia, alt. approx. 3000 ft., *Epling and H. Offord* 8226 in 1925 (CRB); St. Maries River near Clarkia, *C. R. Quick* 1130 in 1933 (CRB); Upper St. Maries River, St. Joe Forest, around Clarkia, alt. 4000 ft., *W. W. White* 41, 42, 43, 45, 56 in 1933 (FS 70624-70628). BENEWAH CO.: Emerald Creek, alt. 3000 ft., *White* 38 in 1933 (FS 70623). KOOTENAI CO.: Fernan Lake, Coeur d'Alene, *Henry J. Rust* 502 in April, 1913 (CRB, USN). BONNER CO.: South end of Chase Lake at Lost Creek, south of Coolin, *Christ* 17957, 17961 in 1948 (CRB); in Bismark Meadows, 2 miles south of Nordman, *Christ* 17984 in 1948 (CRB); Priest River, alt. 2700 ft., *Epling* 7932 in 1925 (CRB); West Fork of Priest River, *J. B. Leiberg* 2841 in 1897 (USN); Priest Lake, C. V. Piper 7, 8, 9, 10 on Aug. 28, 1916 (CRB, WSC); Priest Lake, *Piper* 3742 in Aug., 1901 (USN, WSC); East Fork of Priest River near Coolin, *Piper* 6611, 6620, in 1923 (CRB, WSC); Foot of Priest Lake, Coolin, *Piper* 6616b (WSC), 6633 (CRB, WSC) in 1923; Head of lower lake, *Piper* 6634, 6637, 6648, 6649, 6650, 6651 in 1923 (CRB, except 6634 and 6648; all WSC); Kaniksu National Forest, alt. 2400 ft., *White* 2 (FS 69173) in 1926 (CRB), *White* 2 in 1926 (FS 69174). BOUNDARY CO.: Bonners Ferry, *Christ* 3691 in 1934 (CRB); Kaniksu Forest, Moore's Creek bridge, alt. 2400 ft., *White* 1934-b in 1934 (FS 71206). COUNTY UNKNOWN: North Fork of Coeur d'Alene River, *Leiberg* 1533 in 1895 (USN); Headquarters, *Epling*, in July, 1929 (CRB); Jansville (or Jairsville), *Piper* 2919 in July,, 1898 (WSC).

OREGON. COUNTY UNKNOWN (probably Union or Wallowa): Wet subalpine meadows, *Wm. C. Cusick* 1302a in 1886 (USN).

WASHINGTON. WHITMAN CO.: "6 miles east of Pullman" (type locality), *Piper* 2922 on Apil 30 and July 2, 1901 (CRB and CUA, 2 sheets each; USN); *Piper* 3590 on April 13 and Sept., 1901 (CRB, CUA, USN).

ALBERTA. Waterton Lakes Park: alt. 4200 and 5000 ft., respectively, *Malte and Watson* 116759 (257), 116764 (341), in 1925 (CRB). Crows-nest Pass area: *J. Macoun* 94322 (7) in 1897 (CRB); *W. C. McCalla* 6831 in 1943 (CRB). Castlemount River (west branch of): *Malte and Watson* 116951 (2486) in 1925 (CRB). Rocky Mountains Park (Banff area): *McCalla* 6500, 6524 in 1941 (CRB); *N. B. Sanson* 16, 255, 259, 2077 in 1911, 39 in Aug., 1942 (all CRB). In Rocky Mountains, Nordegg, *Robt. G. H. Cormack* 793 in 1945 (CRB). Lake Louise Area: alt. 5700 ft., *Edith M. Farr* 1056 in 1905 (CRB, as *S. pellita*); *Malte and Watson* 116824 (1092) in 1925 (CRB). Jasper Park: *J. G. Jack* 2623, 2640, 2773 in 1922 (CRB). Athabaska River at Athabaska (Landing), *C. R. Ball* 2364 in 1925 (CRB, 2 sheets).

BRITISH COLUMBIA (southeastern): Elk River valley at Fernie, *McCalla* 6840 in 1942 (CRB). North side of Wapta Lake, *J. Macoun* 68890 in 1904 (CRB).

3. **S. Drummondiana** Barratt, variety **subcoerulea** (Piper) n. comb.
Salix Covillei Eastwood, in Zoe 5: 80. 1900.

S. pachnophora Rydberg, in Bull. Torrey Bot. Club 31: 403. 1904; Rydberg (Fl. Colorado), in Colo. Agric. Expt. Stat. Bull. 100: 95. 1905; Rydberg, Fl. Rocky Mtns. and Adjac. Plains 197. 1917.

S. pellita, at least in part, as interpreted by Ball (Notes on West. Willows), Trans. Acad. Sci. St. Louis 9: 81-82. 1899; Farr (Contrib. Cat. Fl. Can. Rocky Mtns. and Selkirk Range), in Contrib. Bot. Lab. Univ. Penna. 3(1): 31. 1907; Nelson (Elias E., Shrubs of Wyo.), in Wyo. Agric. Expt. Stat. Bull. 54: 9. 1902, not Andersson.

S. subcoerulea Piper, in Bull. Torrey Bot. Club 27: 400. 1900; Bailey and Bailey (Woody Pl. Western Natl. Parks), Amer. Midl. Nat. Monogr. 4: 42, 53. 1949; Ball in Coulter and Nelson, New Man. Bot. Centr. Rocky Mtns. 136-137. 1909; Ball in Standley (Fl. Glacier Natl. Park), in Contrib. U. S. Nat. Herb. 22: 320, 323. 1921; Ball in Abrams, Illus. Fl. Pacific States 1: 502, fig. 1222. 1923; Graham (Bot. Studies Uinta Basin), in Ann. Carnegie Museum 26: 166. 1937; Hawkins, Trees and Shrubs Yellowstone Prk. 16mo. 69. 1924; Henry, Fl. So. Brit. Col. and Vancouver Id. 99. 1915; Rydberg, Fl. Rocky Mtns. and Adjac. Plains 197. 1917; Smith (Willows Colo.), in Amer. Midl. Nat. 27: 245. 1942; Tidestrom (Fl. Utah and Nevada), in Contrib. U. S. Natl. Herb. 25: 136. 1925; Van Dersal (Native Woody Pl. U. S.), in U. S. Dept. Agric. Misc. Publ. 303: 253. 1938; Wooton and Standley (Fl. New Mex.), in Contrib. U. S. Natl. Herb. 19: 161. 1915.

Twigs more slender, glabrate-glabrous, often subshining, and, like the buds, usually more or less pruinose; leaves thinner, mostly narrowly oblong-oblanceolate and acute on fruiting twigs, oblong-lanceolate, oblanceolate, or oblanceolate-oval and acuminate on summer shoots, sparsely pubescent or puberulent above, tomentum shorter and less dense beneath than in the species, with the veins more evident, sometimes becoming glabrescent; stipules small or wanting; scales more thinly villous; styles to 1.5 mm. long.

Variety *subcoerulea* has a much more extensive southern distribution than either *S. Drummondiana* or variety *bella*, principally in the wide Rocky Mountain System. It occurs from the mountains of northern New Mexico northward across Colorado (including adjacent Albany Co., Wyoming) and adjacent Utah (Wahsatch and Uinta Ranges), the western parts of Wyoming and Montana, most of Idaho, eastern Oregon (Harney, Union, and Wallowa Counties), and northeastern Washington (Spokane and Okanogan Counties). In Canada, it occupies the mountainous adjacent portions of Alberta and British Columbia to about Lat. 56°N. There is a sparse southwestern distribution across Nevada to Inyo and Tulare Counties in the southern Sierra Nevada of California.

In the southern mountains, variety *subcoerulea* occurs at altitudes ranging from 6000 to 10000 or 11000 feet, with progressively lower elevations northward, usually from 3000 to 7000 feet in Canada. The flowering and fruiting periods are about the same as for the species and variety *bella*. In its southern range, the higher altitudes counteract the usual effects of the more southern latitudes.

Collections are cited here from only the northern part of its range, where its distribution overlaps that of the species, or variety *bella*, or both. This area covers northwestern Montana, the northern tip of Idaho, and the adjacent portion of Washington, together with the total area occupied in Alberta

and British Columbia. In these Provinces, variety *subcoerulea* extends northward to about 56°N., which is farther north than either the species or variety *bella* are found, especially the latter in British Columbia. Although variety *subcoerulea* occurs in northeastern Oregon, no specimens are cited here even though one specimen of variety *bella* from there is cited. The abbreviations of the names of containing herbariums are the same as previously given.

The difficulty of being completely sure of the identity of juvenile specimens should be re-emphasized here. It is quite probable that the writer himself would change some determinations in any future inspection of this material and even more certain that others will do so. We can be sure, however, that they all belong within the species.

MONTANA. MISSOULA CO.: Camas Prairie, in Blackfoot Valley 20 miles ne. of Bonner, *C. L. Hitchcock* 1552 in 1933 (CRB). GLACIER CO.: Summit (border of Glacier Natl. Park), *H. L. Shantz* on May 19, 1926 (CRB, 2 sheets; USN). FLATHEAD CO.: Columbia Falls, *R. S. Williams* 972 in 1893 (USN. pist. aments 8-9 cm. long). Glacier National Park: *Vernon Bailey* at Lake McDonald, on Aug. 29, 1917 (USN); *Bassett Maguire et al.*, at various points, 5275, 5278, 5281, 5283, 5306 in 1934 (all CRB); *Paul C. Standley*, at various localities, 14961,16864,16885,17311, 17342, 17642, 18127 in 1919 (all USN).

IDAHO. SHOSHONE CO.: On Heller Creek, 6 mils southeast of Red Ives Ranger Station, *J. H. Christ* 17063 in 1947 (CRB); Coeur d'Alene Natl. Forest, Magee Ranger Station, alt. 3000 ft., *Wilfred W. White* 374 in 1935 (FS 94186). BENEWAH CO.: Santa Creek, north of Emida, *Christ and Ward* 7665 in 1937 (CRB); *Christ* 12414 in 1941 (CRB).

WASHINGTON. SPOKANE CO.: Latah Creek, southeast of Spangle, *W. N. Suksdorf* 8638, 8639, 8640 in 1916 (CRB). OKANOGAN CO.: Vicinity of Crawfish Lake, *Charles B. Fiker* 2385, 2386, 2388, 2389, 2392, 2393, 2424, 2425, 2427 in 1937 (all CRB).

ALBERTA. Waterton Lakes Park: alt. 5440 ft., *W. C. McCalla* 6591, 6592 in 1941 (CRB). Castlemount Ranger Station (3 miles east of), alt. 4300 ft., *Malte and Watson* 116780 (535) in 1925 (CRB). Jasper Park: Yellowhead Pass, alt. 3700 ft., *J. G. Jack* 2777 in 1922 (CRB). Slave Lake District: Prairie Creek, *A. H. Brinkman* 4115 in 1929 (CRB); Assineau River, *Brinkman* 4349 in 1929 (CRB). Freeman River beyond Fort Assiniboine, *McCalla* 7250 in 1942 (CRB).

BRITISH COLUMBIA. McCullock, high pass between West Kettle River and Okanogan Lake, *Thomas T. McCabe* 5959, 5960, 5961 in 1938 (CRB). Clearwater River Road, 20 miles from North Thompson River Road, 52° N., *McCabe* 1049, 1050 in 1934 (CRB). 25 miles west of Needles, *McCabe* 6675 in 1938 (CRB). Chezacut (Chilcotin) Lake, 52° 20′ N., 124° W., *O. J. Murie* 1326 in 1935 (CRB). Beaver Pass, 53° N., 121° 30′ W., *McCabe* 1076, 1079, 1085 in 1934 (CRB); Devils Canyon Summit, between Stanley and Barkerville, 53° N., 121° 30′ W., *McCabe* 1086, 1087 in 1934 (CRB); Indianpoint Lake, 25 miles ne. of Barkerville, 53° N., 121° W., *McCabe* 1176 in 1934 (CRB). Summit Lake Road, 8 miles north of Prince George, 54° N., *McCabe* 6944 in 1939 (CRB). François Lake, 54° N., 125° plus W., *J. W. Eastham* 11997 in 1944 (CRB). 25 miles south of Ft. St. James, 54° 30′ N., 124° 20′ W., *McCabe* 7587, 7592 in 1940 (CRB). Takla Landing, 55° 30′ N., 126° W., *McCabe* 7865 in 1940 (CRB). Lake Tetana, Driftwood River Valley, 56° N., 126° 30′ W., *Mrs. Theodor E. S. Fletcher* no. C on Sept. 5, 1938 (CRB). Near Fort St. John, 56° 15′ N., 121° W., *E. H. Moss* 2351 in 1931 (CRB, 2 sheets).

The latitudes and longitudes given above are only approximate, in many

cases, but should aid students in visualizing distribution because many of the localities named cannot be found in the ordinary atlas.

B. S. PLANIFOLIA Pursh., var. NELSONII (Ball) Ball, apud Fraser & Russell

There have been certain uncertainties concerning this variety and its previous specific status. Therefore it seems desirable to cite discussions of it, correct items in the description, and list numerous specimens representing it.

S. chlorophylla Andersson, in part, as interpreted by many western authors, in so far as specimens with very narrow leaves are included.

S. Neloni(i) Ball, in Bot. Gaz. 40: 379 (-380), pl. 13. 1905; Ball, in Coulter & Nelson, New Man. Bot. Centr. Rocky Mtns. 137. 1909; Ball (Notes on N. A. Willows III), in Bot. Gaz. 60: 397-398. 1915; Farr (Contr. Cat. Pl. Can. Rocky Mts. & Selkirk Range), in Contrib. Bot. Lab. Univ. Penn. 3 (1): 31. 1907; Hawkins, Trees & Shrubs Yellowstone Park 67. 1924, 16mo.; Rydberg, Fl. Rocky Mts. & Adjac. Plains 198. 1917; Schneider (Notes on Amer. Willows VI), in Jour. Arnold Arb. 1: 80-81. 1919; Schneider (do. XII), ibid. 3: 77 (footnote). 1922; Tidestrom (Fl. Utah & Nev.), in Contrib. U. S. Natl. Herb. 25: 137. 1925.

S. planifolia Pursh, var. *Nelsonii* (Ball) Ball, apud. Fraser & Russell, A Revised, Annotated List of the Plants of Saskatchewan 23. 1944 ("Salix planifolia Pursh var. Nelsonii Ball—S. Nelsonii Ball. Differs from the species by its narrow, pointed leaves."); Breitung (Cat. Vasc. Pl. Centr.-East. Sask.), in Can. Field Nat. 61: 84. 1947; Smith (Willows Colo.), in Amer. Midl. Nat. 27: 246. 1942 ("Salix planifolia var. Nelsonii Ball, Bot. Gaz. 40: 379. 1905. Now considered by Ball as a variety (personal letter)."). *nomen nudum;* Turner (Pl. Edmonton Dist., Alta.), in Can. Field Nat. 63: 10. 1949.

Differs from the species in leaves narrowly oblanceolate or sometimes narrowly lanceolate or narrowly elliptical, acute at both ends or the base sometimes cuneate, 3-6 cm. long on flowering and fruiting twigs or to 7 or 8 cm. long and 1.3-1.8 cm. wide on vigorous foliage shoots, entire or the larger sparsely and shallowly glandular crenate-serrulate; stipules none, or small and early deciduous.

The original description was based on limited and some not properly developed material. It should be noted, therefore, that the pistillate aments may become 5 cm. long. The styles, described from imperfect specimens as 0.3-0.5 mm. long, normally range from 0.6-1.2 mm. in length and the stigmas are somewhat shorter.

The writer published *S. Nelsoni(i)* in 1905, before he had learned how painstakingly the willows must be studied. For several years, however, he has recognized this narrow-leafed plant as being only a variety of *S. planifolia* and has so determined scores of specimens for collectors. Unfortunately, the publishing of the new combination was overlooked. The first author to use the varietal combination in print apparently was Smith, in 1942 (l.c. above), but he neglected to give the specific name as a synonym although he cited the place of its publication. The varietal combination therefore was not validly published by him. The first authors to do this were Fraser and Russell, in 1944, as noted.

The pistillate type is Nelson 7580, from Laramie Peak, Albany Co., Wyo., in 1900, in Herb. CRB. Because the species is precocious in flowering, it is almost impossible to recognize staminate plants of the variety while in flower. This causes a scarcity of authentic staminate specimens in herbariums, as noted by Schneider in 1919. The remedy lies in tagging staminate plants and collecting flowering specimens then and foliage specimens later, when identification is possible.

Variety *Nelsonii* is found practically throughout the range of the species. It occurs rather commonly in the broad Rocky Mountain System of Colorado, South Dakota, Wyoming, and western Montana, and adjacent Alberta. It occurs rarely in NE. Utah, SE. Idaho, and central British Columbia, more commonly in central Alberta and Saskatchewan, less commonly in their northern parts and in Mackenzie, and rarely in Ontario (Hudson Bay), Ungava, and Labrador. In the mountains of Colorado, it reaches elevations of 11,000-12,000 feet, with progressively lower maximum altitudes northward, until nearly sea-level is reached at Hudson Bay and eastward.

COLORADO. EL PASO CO.: Little Fountain Cr., *J. C. Blumer* 12, in 1903 (CRB); Pikes Peak, *J. H. Christ* 1164, in 1935 (CRB). TELLER CO.: Rosemont, *Christ* 2243, in 1936 (CRB). EL PASO OR TELLER CO.: Pikes Peak For. Res., *S. J. Flintham* on Ang. 18, —— (USN); Pikes Peak, Alpine Lab., 10,000 ft. elev., *C. J. Whitfield* 17, in 1931 (CRB). PARK CO.: Mt. Lincoln, 12,000 ft. elev., *J. M. Coulter*, July 9, 1873 (USN). LAKE CO.: between Twin Lakes & Leadville, *Christ & Ward* 2442, in 1936 (CRB). OURAY CO.: Mt. Ouray, *Pammel & Dudgeon* 28 in 1905 (CRB). LARIMER CO.: Rocky Mtn. Natl. Park, *Christ* 727, in 1935 (CRB); Beaver Cr., *L. N. Goodding* 1440, in 1903 (CRB); Estes Park, *E. C. Smith* 257, 259, in 1933, 287, 377, 378, in 1934, & 1438, in 1940 (all CRB); Poudre Lakes, 10796 ft. elev., *Smith* 1473, in 1940 (CRB); Longs Peak Inn, *Smith* 1644, in 1943 (CRB). JACKSON CO.: Rabbit Ear Pass, *Smith* 419, in 1934 (CRB); North Park, Walden, *Smith* 928, in 1937 (CRB). ROUTT (?) CO.: Routt Nat. For., 6700 ft. elev., *Roscoe B. Weaver* 145, in 1914 (CRB). COUNTY UNKNOWN: Peak Valley, elev. 3800 m., *F. E. & E. S. Clements* 310, in 1901 (USN).

UTAH. DUCHESNE CO.: Mt. Emmons, Uinta Mts., 11,000-11,350 ft., *F. J. Hermann* 5011, 5028, 5170, in 1933 (CRB).

SOUTH DAKOTA. LAWRENCE CO.: (Black Hills), *W. H. Over* 16359, in 1924 (CRB). PENNINGTON CO.: near Deerfield, *A. C. McIntosh* 851 in 1921 (CRB); *Over* 16355, in 1924 (CRB); B. H. Natl. For., headwaters of Jim Creek, *T. C. Setzer* 3, in 1913 (CRB).

WYOMING. ALBANY CO.: Laramie Peak, *A. Nelson* 7580, in 1900 (CRB, type; USN); Nashs Fork, *Nelson* 7779, in 1900 (CRB); Centennial, *Nelson* 1754, in 1895 (USN); *Nelson* 8822, in 1902 (CRB, USN); Laramie Hills, elev. 8500 ft., *L. O. Williams* 2200, in 1935 (CRB, USN). SHERIDAN CO.: West Br. Big Goose Cr., elev. 8500 ft., *Pammel & Stanton* 220, in 1897 (CRB); *Frank Tweedy* 47, in 1893 (USN). JOHNSON CO.: Big Horn Mts., headwaters of Clear Cr. & Crazy Woman R., *Tweedy* 3438, in 1900 (USN); No. Fork Powder R., alt. 9000 ft., *L. O. & Rua Williams* 3126, in 1936 (CRB). WASHAKIE CO.: Highway 16 in Big Horn Mts., *Carleton R. Ball* 2901, 2904, 2907, in 1939 (CRB, USN). BIG HORN CO.: West Tensleep Cr., alt. 9000 ft., *L. O. & Rua Williams* 3140, in 1936 (CRB). SUBLETTE CO.: Big Horn For., So. Fk. Piney Cr., alt. 7800 ft., *S. R. Long* 229, in 1912 (CRB, FS 22274). TETON CO.: Two Ocean Lake, *O. Murie* 193, in 1928 (USN); Grand Teton Natl. Park, elev. 7500 ft., *Williams* 1194, in 1933 (CRB); Double Diamond Ranch, *Williams* 3500, in 1937 (CRB). Yellowstone Natl. Park: near Lower Geyser Basin, *Ball* 2167, in 1923 (CRB, USN); *E. A. Mearns* 3125, in 1902 (USN).

MONTANA. CARBON CO.: near Beartooth Pass, so. of Red Lodge, elev. 9400 ft., *P. L. Ricker* 6398, in 1946 (CRB). GALLATIN CO.: near Madison R., nw. of Grayling, *Ball* 2917, in 1939 (CRB, USN). MEAGHER CO.: Helena Natl. For., Birch Cr., *Wilfred W. White* 335, in 1939 (CRB, Fs 95161). MISSOULA CO.: Camas Prairie, Blackfoot Valley, 20 mi. ne. of Bonner, *C. L. Hitchcock* 1553, in 1933 (CRB).

BRITISH COLUMBIA. Chezacut (Chilcotin) Lake, *O. J. Murie* 1319, 1325, in 1935 (CRB). ALBERTA. Banff & Vicinity: *W. C. McCalla* 2253, in 1899 (USN); *McCalla* 6444, in 1941 (CRB); *N. B. Sanson* 72, 76, 100, 153, 154, 160, 163, 204, 223, 238, 305, 378, 394, 423, 446, 447, 2070, 2074, all in 1911 (all CRB). Elbow R. Valley, Calgary, *McCalla* 6811, in 1942 (CRB). 30 mi. se. of Calgary, *McCalla* 9094, in 1946 (CRB). Smith Landing, *H. V. Radford* 10, 57, in 1911 (CRB). Rt. Saskatchewan and vic., *George H. Turner* 15, in 1928 (CRB); 1150A, 1150B, 1189 1236, 1260, in 1939 (all CRB). MACKENZIE. Great Bear Lake, *Hansford T. Shacklette* 3054, in 1948 (CRB).

SASKATCHEWAN. Cypress Hills, *A. J. Breitung* 5121, 5210, in 1947 (CRB); *Robert G. H. Cormack* 542, in 1945 (CRB). McKague & vic., *Breitung* 543, 552, 553, 830, in 1940 (CRB); *Breitung* 910, 1499, in 1941 (CRB). LAKE ATHABASKA: *McFarlane R., H. M. Laing* 224, in 1920 (CRB); Charlot Point, *Hugh M. Raup* 6147, in 1935 (CRB); Ennuyeuse Cr., *Raup* 6944, in 1935 (CRB); Candle Lake, 60 miles ne. of Prince Albert, *Boivin and Breitung* 6081, in 1949 (CRB). ONTARIO. Moosonee, *Dutilly and Lepage* 12056, in 1944 (CUA); Weenusk, Hudson Bay, 55° 15′ N., *Dutilly and Lepage* 16897, in 1946 (CRB). QUEBEC. Ungava, Larch River, approx. 57° N., *Dutilly and Lepage* 14510, in 1945 (CRB). LABRADOR. Cape North, near Cartwright, approx. 53° 30′ N., *G. Gardner* 240, in 1938 (CRB).

A Natural Hybrid of Liatris (x L. Weaveri Shinners)[1]

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Natural hybrids have been frequently mentioned in botanical literature. Some have been described and checked by cytological analysis. Others have proved authentic since it has been possible to resynthesize the hybrid from the putative parents. In composites, with heads of small perfect florets, conclusive hybridization results are not readily accomplished, even though the plants are almost self-sterile. Allan (1940) who has reported many wild hybrids in New Zealand stated "Certainly field evidence is circumstantial only but it is often so overwhelming as to leave no doubt in an unprejudiced mind." Nevertheless, the acceptance of such hybrids, as have not been reproduced experimentally, is still questionable. Additional weight is frequently added, however, by knowing the cytology and comparing it with that of the two species between which they seem intermediate.

Along with other cytological studies in *Liatris* has been included that of a plant which had been determined as a hybrid by Shinners (1943). The specimens named x *L. Weaveri* by him, were seen in the Missouri Botanical Garden where they had been deposited by B. F. Bush.[2] These had been sent to him by the author in 1933 along with other *punctata* accessions when they had proved puzzling among plants of the population from whence they arose.

Origin

Seed received late in 1926 from Dr. E. J. Weaver, Lincoln, Nebraska, was the source of *L. punctata* Hook. var. *nebraskana* (accession No. 10) which was reported as diploid, Gaiser (1950). Neither those first nor any subsequent seedlings varied noticeably (Pl. I, A). From another envelope, received at the same time from the same locality, seedlings were grown in the two following years and two populations (No. 7 and No. 7a) were obtained. Though no herbarium specimen accompanied the seed packet, later Dr. Weaver sent along three sheets, of Aug. 30, 1928, upland prairie, Lincoln, Nebraska, which have been identified as *L. aspera* Michx. var. *typica*.

When the 1927 seedlings came into bloom in their second year, as is characteristic of *Liatris*, most were *aspera-like*, as the plant to the right in Pl. II, A, but one (subsequently No. 16) was distinctly different in leaves, flower arrangement, size and shape of heads and phyllaries. In the second population of 1928, another plant (thereafter No. 17) was found to be very similar in habit to the former variant though the phyllaries were a little less obtuse

1 The author is indebted to Dr. K. Sax for helpful criticism of this paper.

2 By letter to the author.

(plant to left in Pl. II, A). When all had bloomed, a third was found (7 plant 4). In the summer of 1930, the record was made that the somewhat lanceolate phyllaries were green, without color, in contrast to the colored bracts of the other seedlings and were *punctata*-like (cf. Pl. I, A). One stem of each of seven seedlings, including the three variants on the left, is shown in Pl. I, B. Later, further resemblance to *L. punctata* was seen in the more numerous short stems having almost spicate inflorescences, of all three of these plants. The remainder produced one to three taller stems with the characteristic, more distributed, larger, globose heads of *L. aspera*. The differences are clearly shown in the photographs (Pl. I, C and 11 B) of the plants as they appeared in 1933. In Pl. II, B one of the usual *aspera*-like plants is shown to the right. Hereafter the three plants will be referred to as hybrid-like.

CYTOLOGICAL OBSERVATIONS IN THE POLLEN-MOTHER-CELLS

(a) Of *aspera-like seedlings*.—By the summer of 1933, when a number of both the 1927 and 1928 seedlings had come into bloom, it was possible to study the chromosome number at meiosis in six of eight plants of the former (No. 7) and five of ten plants of the latter (No 7a), including the three hybrids. Some plants did not flower. Those produced only radicle leaves or dwarfed stems. The same method, as used in previously published *Liatris* studies, of preparing and drawing from aceto-carmine mounts which were made permanent as a source of reference, were followed. These, with the herbarium specimens have recently been rechecked for the following results shown in Table I.

In one plant of each population the haploid chromosome number was 10 (fig. 1, 2) and in all others examined meiotically it was 11 (fig. 3-11). Thus two similar appearing *aspera*-like plants, standing next to one another, could have the varying numbers of 10 and 11 respectively (see Pl. I, B).

In the numerous fine division figures seen with 11 units, it was possible when the chromosomes were well separated to say that two or three were smaller than the others, as in fig. 7, but when the units were a little more crowded (fig. 3, 4) the similarity of size and shape of them all made such determination uncertain. When chromosomes lie freely in the cytoplasm the diameter of some may be less if already slightly elongated in metaphase-separation. Comparison of equally well spread out units in a 10- and an 11-chromosome plate (cf. fig. 1, 2 & 7), makes it uncertain whether the additional chromosome is one of smaller rather than of the larger size. There was no evidence of multivalent associations. The divisions appeared quite regular. In lateral views of the spindle, one bivalent (fig. 5a) or two (fig. 6a, 6b) or three (fig. 7a) were occasionally seen as just splitting, with the two units separating or moving off to the poles a little in advance of the other chromosomes. They never seemed to lag behind the two main metaphasic groups. From late anaphase figures (fig. 3a) no lagging chromosomes were seen and by telophase stages, all units seemingly had been included in the daughter nuclei. Second divisions also proceeded regularly (fig. 5b, 8).

TABLE I.—Chromosome nos. and fertility in seedlings from "aspera" seed from Lincoln, Nebraska, 1926

Aspera-like plants *1927 seedlings No.*	n	2n from germinated seeds	% of unfilled seed	No. of seeds germinated in 50	Germination % of
7 pl 5	10	20	very low	20	40
7 pl 3	11	22	very low	12	24
7 pl 6	11	22	very low	28	56
7 pl 2	11	22	high	9	18
7 pl 7	—	20			
1928 seedling					
7a pl 7	10	20	very low	31	62
7a pl 8	11	22	very low	26	52
7a pl 1	11	22	intermediate	14	28
7a pl 3	11	22	intermediate	10	20
Hybrid plants					
1927 seedlings					
16	11	22	very high	23	46
7 pl 4	11	—	very high	16	32
1928 seedlings					
17	11	22	very high	25	50

(b) *Of hybrid-like seedlings.*—In these three plants (16, 17 and 7 plant 4), the chromosome count was repeatedly 11 (fig. 9, 10, 11). Thus regardless of whether plants appeared typical or hybrid-like they might have the same number. For example, the two dissimilar plants of *aspera-* and hybrid-like appearance, shown in Pl. II, B, each had 11 chromosomes.

In plant 17, meiosis was a little less regular than was generally found. Some of the bivalents appeared heteromorphic at the early plate stage when the chromosomes were still somewhat scattered (fig. 11a). Asynapsis or early separation of one or two chromosome pairs was occasionally seen. This was the only seedling in which one or two chromosomes were observed to divide late and lag on the spindle (fig. 11b, c) appearing as though they might be left out of the daughter nuclei. Though this might have occurred sometimes, it was not seen and certainly on some II M plates there were 11 chromosomes each (fig. 11d). In another cell (fig. 11e) it was a little less certain that each plate had 11, though the one suggesting only 10 appeared to have another immediately underlying one unit. In plant 16 (fig. 9a) no irregularities were noted other than asynapsis or earlier splitting of one to three bivalents. Though not as many stages were studied in 7 plant 4 (fig. 10), sometimes arrangements at early metaphase was a little more uneven, as it had been in plant 17 (fig. 10a cf. fig. 11a).

(c) *In root-tips.*—The constancy with which 11 units were found, made it unlikely that this number was merely the result of asynapsis of one pair of chromosomes. However it was desirable to check on the somatic numbers. Not anxious to disturb the well-rooted plants to obtain root-tips, seeds of all plants were germinated instead, both to obtain somatic figures and as a test of their viability. From root-tips of growing seeds, it was possible to check on eleven of the plants in this way. Without exception, for all in which the gametic chromosomes had been previously seen, the diploid number corresponded exactly to that of the haploid (see Table I). Thus nine plants which had eleven chromosomes at meiosis, were considered aneuploid ($2n=22$). In contrast, two plants were regular diploids ($2n=20$). One other plant, which had not been examined meiotically and which died the next winter, would probably have had that number too, as root-tips of its germinated seed had 20 chromosomes.

SEED-SET AND GERMINATION

Fertility of these plants was variable as judged when sorting seeds for planting 50 of each in December 1933. A report of these germination results is also included in Table I.

It was more obvious than the table shows that the three hybrids were least fertile, for from such large bushy plants of over twenty stems each, as seen in the photographs, almost all the seeds were white or greenish and unfilled, so that it was difficult to obtain even the 50 desired seeds. It is possible that since the finding of any filled seeds among them was so distinctive, only truly good ones were selected for these plants. Three other plants, although showing more filled seeds than the hybrids, had also been recorded as being of intermediate fertility and their germination percentages proved lowest. They were three having the aneuploid number. The germination results were quite variable, ranging from 18 to 62%, with the hybrids showing comparatively high percentages of 46, 52, and 32, which may have an explanation in the more clear-cut sorting of good seeds. The highest germination was from one of the plants having 10 chromosomes but the other having that number gave 40%.

The seedlings were transferred from the greenhouse to a garden at Crediton, where there may have been more loss than ordinarily would have occurred, through the combination of the very hot dry summer of 1936 and pressure of other work that gave them little attention that season. By the summer of 1938 many of the plants were well developed and could be compared with populations of typical *L. aspera* from Minnesota (No. 1) and *aspera* var. *intermedia* from Arkansas (No. 64) (ms. in prep.) as well as with the parent plants. For the most part the stand was a rather uniform *aspera*-like population for each except those of the three hybrids where the pattern of strikingly lower, bushy, many-stemmed plants of narrower leaf and different spike and head characters gave three blocks of plants that for the most part resembled *L. punctata*. Only a few in each plot resembled *L. aspera*. The photographic record depended upon for showing this contrast was unfortunately a blank.

CYTOLOGY OF PROGENY OF THE SEEDLINGS

Though it was not possible to do more than make a sampling for cytological sutdy of this large number, meiotic chromosomes of 26 seedlings were seen and drawn and these results have been tabulated in Table II. While cytological examination of one seedling of a group is insufficient, it is acknowledged, still it was hoped by such scatter testing to see if the chromosome numbers of the progeny had remained generally similar to the parental, whether 2n or 2n+2.

TABLE II.—Chromosome numbers in a sampling of progeny of the seedlings

Progeny of hybrid-like					Progeny of *aspera*-like			
No. of parent plant	n = in parent plant	No. of seedling plant	n = in seedling plant	2n	No. of parent plant	n = in parent plant	No. of seedling plant	n = in seedling plant
7 pl 2	11	6	11		16	11	3	11
7 pl 2		7	11		16		11	11
7 pl 3	11	1	11		16		13	11
7 pl 5	10	10	10	20	16		17	11
7 pl 6	11	16	11		17	11	1	11
7a pl 1	11	5	11		17		3	11
7a pl 1		6	11		17		4	10
7a pl 1		9	11		17		6	11
7a pl 3	11	4	11		17		7	11
7a pl 7	10	2	11		17		19	$3+16_1$
7a pl 8	11	10	10		17		22	11 or $10+2_1$ or $8+4_1$
7a pl 8		20	10		17		24	11
7a pl 8		21	10		7 pl 4	11	5	10
7a pl 8		22	15, 16, or 17		7 pl 4		14	$4–5+14_1–12_1$

(a) *From aspera-like seedlings.*—One seedling each of the two *aspera*-like plants with n=10 was checked. While 7 pl. 5 seedling 10 (fig. 12) was as the parent plant had been (cf. fig. 1), the other, 7a pl. 7 seedling 2, differed from its parent showing 11 units both on first (fig. 13) and second division plates (fig. 13a cf. fig. 2).

By examination of at least one, and sometimes two or more seedlings of each of five aneuploid (n=11) *aspera*-like plants (fig. 14-20) the chromosome number was found to be 11. Where there was very striking difference in size of the seedlings as in those of 7a pl. 1, three seedlings including one each of the largest and smallest were studied, but no differences were found (fig. 17, 18, 19). Sometimes, as in the largest one, it was thought there might be 12 chromosomes (fig. 18a) but further examination of this plant gave a beautifully clear well-spaced set of 11 (fig. 18) so that the former

was interpreted as having had one bivalent already separated. However, when in a seedling of 7a plant 8, that had 11 chromosomes, there were only 10 in repeated preparations (fig. 21, 21a), three other seedlings of it were examined. Two more small plants both gave the same number 10 (fig. 22), while a fourth large one obviously had more chromosomes (fig. 23). From I M plates, where 15 to 17 units were counted, it was difficult to determine the exact number of bivalents as it was thought some might have already separated. However, in cells of II M (fig. 23a and b) where the plates were more uniform, the number of units was not more than 16. Lagging chromosomes were seen on these spindle figures.

(b) *From seedlings of hybrids.*—Five of the seedlings of plant 17 were examined in the first year of flowering. At that stage these plants gave considerable surprise. In some, from a rosette of rather broad basal leaves having the appearance and giving promise of developing plants of *L. aspera*, came slender spikes of *punctata*-like arrangement with intermediate heads as can be seen in the two plants (3 and 4) to the right in Pl. II, C. The third seedling to the left is more *punctata*-like in lacking such radicle leaves. It is very like the parent plant had been when of the same age (cf. Pl. II, A). All three are hybrid-like in some characters. Cytologically the two to the left in the picture have the same chromosome number of 11 (fig. 26, 26a) and the plant to the right, had only 10 (fig. 26b and b_1) shown by both polar and lateral views. In a fourth one examined that year, the swollen bivalents were seen as eleven rings (fig. 26c), and in II divisions as two even plates of eleven units each (fig. 26d). For the fifth where a count of 12 was found on one plate (fig. 26e), explanation was found in lateral views of the same. One chromosome pair of 11 was seen to have split well in advance of the rest while a second followed closely (fig. 26f). Again in II division on both plates 11 units were counted (fig. 26g) so that apparently none were lost. In later summers, one of three others examined, showed 11 at I and II divisions (fig. 26h, i). Another showed one to two pairs of univalents (fig. 26j, k). In the third hardly more than three bivalents could ever be found along with numerous univalents so that as many as 19 units were counted scattered over the plate. As in the parent plant 17, there was a greater prevalence for early separation of units or univalents in its seedlings than in those of others.

None of the progeny examined of the second hybrid plant 16, were found to have other than 11 chromosomes on I and II plates (fig. 24, a, b, c, d). However among the pollen grains of one seedling occasional micro grains were noted and in another one an occasional lagging unit was seen on the spindle. Of the two seedlings examined for the third hybrid plant 7 pl. 4, one had again a number of univalents so that there was usually a total of 15 units (fig. 25 a, b). The second plant, chosen because it looked so much like the former one that the same unusual chromosome arrangement was expected, surprisingly had only 10 (fig. 25). This was the third example of reduction to 10 from 11 found in the parent, the first one having occurred among seedlings of an *aspera*-like plant.

It may have been so in more cases had there been time to examine more plants of each.

SEED-SET OF PROGENY

In October of 1938 the then remaining progeny of the three hybrid plants, were checked for seed-set. Only a few seeds were found in any plant except 7 plant 4 seedling 5, which fortunately had been studied meiotically and the chrosomes drawn. This was the plant that had shown n=10. The poor fertility of these plants is shown in Table III.

TABLE III.—Fertility of progeny of hybrid plants in summer of 1938

	Original No. of seedlings	No. of plants that had died since 1934	No. of plants failing to bloom in 1938	No. of plants failing to set any seed, 1938	No. of plants setting very little, 1938*
of No. 17	25	9	1	11	4
of No. 16	23	15	1	7	0
of 7 pl 4	16	6	2	5	3*

* Only one plant (7 pl 4 seedling 5) gave a good seed set, and it had 10 chromosomes.

DISCUSSION

That three strikingly noticeable variants were observed among the seedlings obtained in two successive years from a packet of seeds of *L. aspera* collected where a second species, *L. punctata* var. *nebraskana*, was native, suggests natural hybridization. The circumstantial evidence lies in the intermediacy of the three plants between these two species and in the resemblances of their seedlings to both species.

By examination of both varieties *typica* and *intermedia* of *L. aspera* from other sources (ms. in prep.) as well as of variety *nebraskana* of *L. punctata*, the chromosome number of each was that common to most of the genus (n=10). However for this accession of *L. aspera* the same number was found only in two of the eight *aspera*-like seedlings examined meiotically. The same number would probably have been found in at least a third, since the somatic number from germinated seed of that plant was 20. Since all of the plants were not studied cytologically it is impossible to state it as a percentage. However in the majority examined (six of these *aspera*-like seedlings) there were 11 (n+1) chromosomes at meiosis and 22 in mitotic divisions of root-tips from their germinated seeds. None of the first seedlings really have the n+2 number though several preparations had suggested it. In two of the subsequent seedlings there was found a larger number of units probably due to increased failure of pairing.

Because of the general lack of morphological and size differences in meiotic chromosomes of *Liatris*, it was impossible to recognize the origin of the extra chromosome in the haploid genom. This was also true for the mitotic figures. The original addition of one chromosome to the basic haploid set of *L. aspera* could be explained by non-disjunction in the meiotic process when one of the chromosomes along with its homologue

passed to the same pole and after second division became a part of an n+1 or 11-chromosome gamete. If such a pollen grain in turn fertilized a similar egg cell, the zygote would have become 2n+2. Since a majority of the plants studied showed this aneuploidy, it seems reasonable to assume that the seed packet contained seeds gathered from at least two different plants, one 2n=20 and another 2n=22.

Aneuploid numbers have not been found elsewhere in *Liatris*. Polyploidy too is rare but occurs in one of ten series, the *Punctatae*. Thus in the genus, which is generally of the *Pinus* type (Tischler 1929) with species having the same chromosome number, aneuploid and multiple euploid numbers have made a beginning. Afzelius (1924) found about equally rare aneuploid numbers in two of forty species in the otherwise polyploid series of *Senecio*.

If non-disjunction of one of the bivalents in *L. aspera* gave rise to an aneuploid, which would thus have the two homologues of a pair, the similarity of the progeny having an extra chromosome to those of a normal diploid, might find an explanation. That the three plants which were definitely hybrid in appearance should have the same aneuploid number is more difficult to explain. They could be the result of the successful fertilization of an (n+1) *aspera* gamete by (n) pollen of *L. punctata*. This has some ground of possibility in the experimental production of hybrids between the 9- and 10-chromosome *Nicotiana* species. Avery (1938) described successful hybrids between *N. longiflora* (n=10) and both *N. alata* (n=9) and *N. Langsdorfii* (n=9) even though the morphology of the chromosomes in the karyotypes of the two groups are considered very different. No somatic figures showing a diploid number other than 19 are shown. No direct production of a *Nicotiana* hybrid with an additional chromosome is described. However in the general discussion, Goodspeed (1945) pointed out that the Australian South Pacific Section *Suaveolentes* make up an aneuploid series beginning with 16- and ending with 24- pairs in which the numbers 17 and 23 are lacking. Through hybridization following polyploidy from basic numbers, this series is thought to have been derived. In a total of 73 F_1 interspecific hybrids of which the members of the *Suaveolentes* are parents, the chromosome behavior varied from complete pairing to a lack of it.

In the aneuploid *L. aspera* plants, there was a striking lack of irregularity on the spindle figures except for the early splitting of one, two or occasionally three chromosomes. It was noted that the movement of these units to the poles was always in advance of the rest of the bivalents and all were included in the daughter nuclei. Genetic factors are known to affect chromosome pairing in a number of species (see Sax 1935). Segregation of factors limiting chiasma formation may be responsible for the behavior in these *Liatris* seedlings. Peto (1934) found regular chromosome pairing at meiosis in the F_1 of *Lolium* x *Festuca* but irregular pairing in certain back cross segregates. In the three *Liatris* hybrids, univalents were more frequently seen and occasionally found to lag behind the two anaphase groups. However irregularities were not very conspicuous or numerous. This is in striking

contrast to the condition in one plant of a population of six of *L. acidota* of the *Spicatae* (Gaiser 1949) where lagging units were frequent and varying chromatin masses were not included in the daughter nuclei.

Examination of progeny of the *aspera*-like seedlings showed that their chromosome numbers held for the most part, to that of the parental plants. However one of two seedlings examined of plants having had 10 chromosomes, had 11 chromosomes. This could readily be explained as the result of fertilization by pollen from an aneuploid seedling (n=11). There must have been plenty floating about. That three seedlings of an aneuploid plant should have only 10 chromosomes suggests that one chromosome could also be lost without causing too great unbalance. No evidence of how this occurred was seen. If the extra chromosome did come from non-disjunction, even though it were lost to a cell its homologue would still be left in the genome. In such an instance the loss might not prove too disturbing.

The hybrids produced few seeds. As there were three such plants there would have been opportunity for cross pollination among them. But also there would have been abundant pollen of *L. punctata* and *L. aspera*, either aneuploid or true diploid plants. Their progeny were mostly intermediate to *punctata*-like and sterile. Also in several of them there was a greater failure in pairing.

SUMMARY

x *L. Weaveri* is believed to be a hybrid that arose after aneuploidy had occurred in the parental species of *L. aspera*, from fertilization by pollen of *L. punctata* var *nebraskana*. Meiosis was seen to be quite regular in such aneuploids of 2n+2 and they were quite fertile. Divisions of pollen-mother-cells in the hybrid plants and their progeny showed some, though not extreme disturbances. x *L. Weaveri* did arise in nature and though it must be classed as a hybrid of low fertility it was very vigorous, as shown by the photographs. The plants also proved hardy in a more northern climate where they grew in a garden continuously until 1938 without transfer to the basement for protection against the winter.

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EXPLANATION OF PLATES

PLATE I—A. Seedling *L. punctata* Hook. var. *nebraskana* (no. 10) in first year of bloom. B. Stems of seven seedlings; from left to right, x *L. Weaveri*, 7 plant 4, plant 16, plant 17 (n = 11), *aspera*-like seedlings, 7a plant 7 and 7 plant 5 (n = 10), 7a plant 8 and 7 plant 6 (n = 11). C. x *L. Weaveri*, plants 17 (to left), 16 (to right) in their 5th and 6th years respectively (about 1/6 nat. size).

PLATE II-A. x *L. Weaveri* Shinners, plant 17 (to left) and a seedling of *L. aspera*, no. 7a (to right) in first year of bloom. B. x *L. Weaveri*, 7 plant 4 (n = 11 (to left) and an *aspera*-like seedling 7a plant 8 (n = 11), protographed the same year as Pl. I, C (about 1/9 nat. size). C. Seedlings of x *L. Weaveri*, plant 17, in first year of bloom, from left to right, seedling 1 (n = 11), 3 (n = 11), and 4 (n = 10).

EXPLANATION OF FIGURES

Figs. 1-11.—Meiotic chromosomes of two populations no. 7 (in 1927), and no. 7a (in 1928), from a packet of *Liatris* seed from Lincoln, Neb., as seen in polar views (unless otherwise stated) of first-division*-plate-tages in pollen mother-cells from aceto-carmine preparations drawn by Zeiss apochromatic lenses and camera lucida at approximately 1900 mag., reduced 4/7. Figs. 1-8. of aspera-like seedlings: Fig. 1. 7 pl.* 5. Fig. 2. 7a pl. 7. Figs. 3, 3a. 7 pl. 2, I M, I anaphase. Fig. 4. 7 pl. 3. Figs. 5, 5a, 5b. 7 pl. 6, I, M. lateral I M, II M. Figs. 6, 6a, 6b. 7a pl. I, I M, lateral I M. Figs. 7, 7a. 7 pl. 3, I M, lateral I M. Fig. 8. 7a pl. 8, one plate of II M. Figs. 9-11. of hybrid-like seedlings = X *L. Weaveri:* Figs. 9, 9a. pl. 16. Figs. 10, 10a. 7 pl. 4, I M, early metaphase. Figs. 11, 11a, 11b, 11c, 11d, 11e. pl. 17, I M, early I M, I telophase + 1 lagging unit, I telophase + 2 lagging units, II M, II M.

Figs. 12-26.—Meiotic chromosomes of progeny of these seedlings of no. 7 and no. 7a. Figs. 12-23. of aspera-like seedlings: Fig. 12. 7 pl. 5 sdlg.* 10. Figs. 13, 13a. 7a pl. 7 sdlg. 2. I M, II M. Fig. 14. 7 pl. 2 sdlg. 6. Fig. 15. 7 pl. 3 sdlg. 1. Fig. 16. 7 pl. 6 sdlg. 16. Fig 17. 7a pl. 1 sdlg. 5. Figs. 18, 18a. 7a pl. 1 sdlg. 6. Fig. 19. 7a pl. 1 sdlg. 9, 7a pl. 1 sdlg. 8. Fig. 20. 7a pl. 3 sdlg 4. Figs. 21, 21a. 7a pl. 8 sdlg. 10. Fig. 22. 7a pl. 8 sdlg. 21. Figs. 23, 23a, 23b. 7a pl. 8 sdlg. 22, I M, one plate of II M, one plate of II M. Figs. 24-26. of the X *L. Weaveri* seedlings: Figs. 24, 24a. pl. 16 sdlg. 3, I M, II M. Figs. 24b, 24c. pl. 16 sdlg. 13, I M, II M. Fig. 24d. pl. 16 sdlg. 17. Fig. 25. 7 pl. 4 sdlg. 5 Figs. 25a, 25b. 7 pl. 4 sdlg. 14. Fig. 26. pl. 17 sdlg. 1. Fig. 26a. pl. 17 sdlg. 3. Fig. 26b, b_1 pl. 17 sdlg. 4, I M, lateral I M. Figs. 26c, 26d. pl. 7 sdlg. 7, I M, II M. Figs. 26e, 26f, 26g. pl. 7 sdlg. 22, I M, lateral I M, II M. Figs. 26h, 26i. pl. 17 sdlg. 6, I M, one plate of II M. Figs. 26j, 26k. pl. 17 sdlg. 24.

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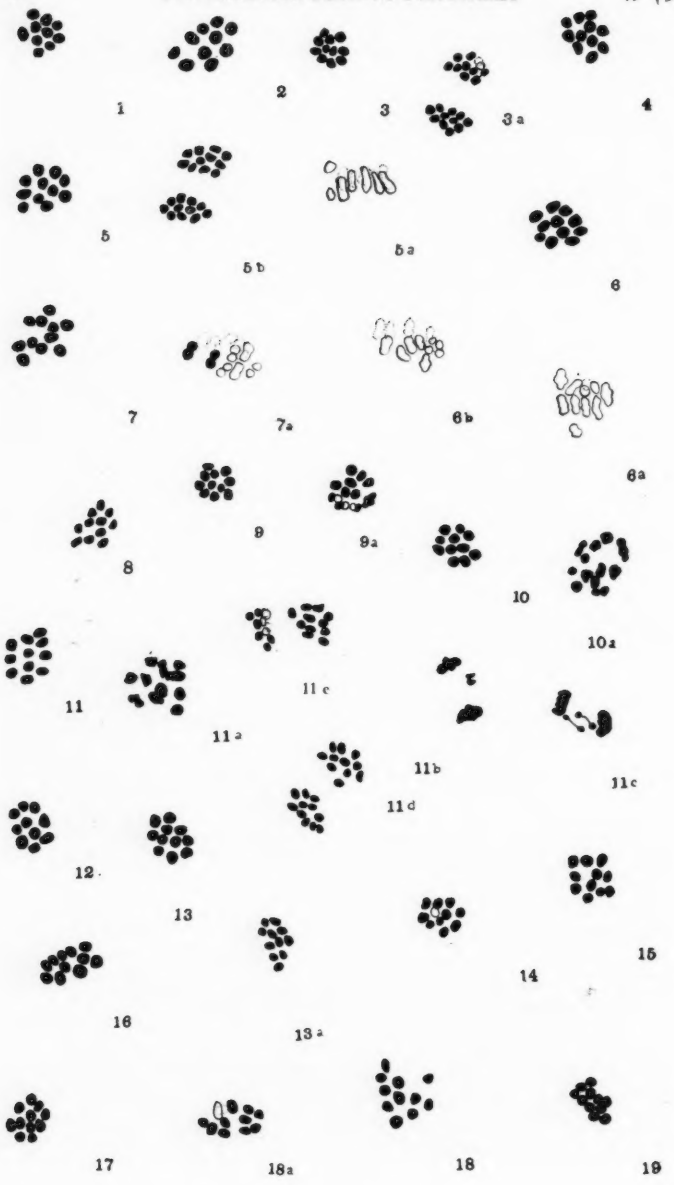
* Abbreviations used: Metaphase plates of first and second division = I M, II M; plant = pl.; seedling = sdlg.

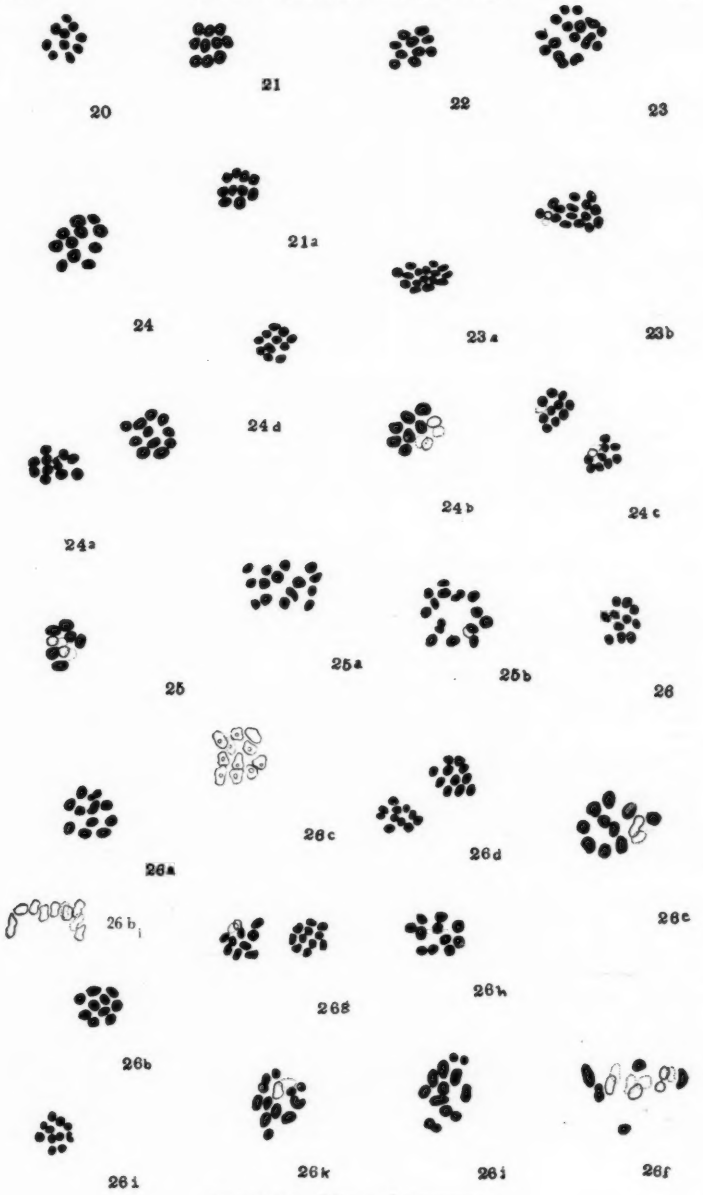
PLATE I

PLATE II

PLATE II



Figs. 1-19.—Meiotic chromosomes.



Figs. 20-26.—Meiotic chromosomes.

BOOK REVIEWS

FAMILIES OF DICOTYLEDONS. By Alfred Gundersen. With introductory chapters by Chester A. Arnold, Oswald Tippo, Theodor Just, Herbert F. Copeland, J. Herbert Taylor, and W. H. Camp. Drawings [about 70] by Maud H. Purdy. 237 pages. Chronica Botanica Co., Waltham, Mass. 1950. $4.50.

The Families of Flowering Plants (1926, 1934) by Dr. John Hutchinson, Royal Botanic Gardens, Kew, is certainly one of the most stimulating botanical books produced in the first half of the twentieth century. This book by Dr. Gundersen is written along somewhat similar lines, and is intended as a compendium of researches in the fascinating field of taxonomy and phylogeny of dicotyledons.

There are twenty-six pages of "Introduction," consisting of short essays by the contributing authors: Fossil Dicotyledons (Arnold), Wood Anatomy (Tippo), Carpels and Ovules (Just), Embryology (Copeland), Cytotaxonomy (Taylor), and Plant Geography (Camp). There follows a six-page commentary by Dr. Gundersen on "characters of dicotyledons," and a few pages of very brief notes on the historical development of plant taxonomy since the seventeenth century. The remainder of the book, nearly 200 pages, is occupied with technical taxonomy.

The 240 families of dicotyledons recognized are grouped into forty-two orders, and ten super-orders or cohorts. The table of contents serves as an outline of the classification followed in the book. The author begins the dicotyledons with apocarpous families. These are followed by families with usually parietal placentation; most "Amentiferae" are placed after Hamamelidales; Ericales are near Theales, Caryophyllales near Primulales, and Umbellales near Rubiales. Thus, the Gundersen scheme is essentially a "ranalian" one, beginning with Ranales (Magnoliales), and ending with Asterales. In a number of ways it resembles the systems of Bessey and of Hutchinson more closely than those of Engler and Wettstein. It follows, for example, the Besseyan plan of distributing some choripetalous families among those with sympetalous corollas. However, the Hutchinson theory of woody-herbaceous evolution of dicotyledons is not emphasized. Chromosome number is given for a few genera. These numbers have been taken chiefly from Darlington & Janaki-Ammal (1945). Each family is provided with a brief summary of the habit of its members, their general geographical distribution, and the number of genera. The family descriptions are brief and mainly diagnostic. Data from wood-anatomy are frequently inserted, as for example "wood hard and durable," "no intraxylary phloem," "vessels absent, growth rings conspicuous," etc. Many families have useful notes, hints, or brief discussion of probable phylogenetic connections, or additional morphological peculiarities. English common names are provided for some (less than half) of the families. The mention of names of representative genera would have added to the usefulness of the book.

In the opinion of this reviewer there are several taxonomic and phylogenetic improvements, such as the placing of Myricaceae in Juglandales, as Warming did, not in a separate order as allocated by Engler, Wettstein, and Hutchinson. Empetraceae are assigned to the Ericales, where, on the basis of general morphology, embryogeny, and development of endosperm, they clearly belong. Following the work of Tippo (1940) Eucommiaceae are grouped with Urticales, instead of Rosales as treated by Bessey and by Engler, or according to Hutchinson, in the Hamamelidales. Salicales are put next to Papaverales; and on the basis of the bicarpellate gynoecium, gynobasic style, single integument, etc., Callitrichaceae (following Schuerhoff, 1926), are placed next to Labiatae. There are, however, a number of assignments, the advantages of which are not immediately apparent, such as the placing of Nymphaeaceae in Magnoliales instead of Ranales. Incidentally, why maintain Magnoliales as an order if the Hutchinson emphasis upon the theory of woody-herbaceous evolution is not adopted? The aquatic or paludal Elatina-

ceae, with axial placentation and stipulate leaves, are placed in Tamaricales, which are said to consist of "Dry climate plants, leaves small, exstipulate, plac. parietal." Hutchinson's assignment of this family to the Caryophyllales seems a better solution.

One of the good features of the book is its uniformly excellent illustrations. About one-quarter of the families are illustrated by clear, bold, apparently mostly original drawings showing details of structures of flowers, frequently with emphasis on the structure of flower-buds to show probable phylogenetic trends. There are about seventy of these illustrations, each consisting of several figures. There is a compact, ten-page bibliography consisting with few exceptions of publications more recent than 1925. The book appears to be nearly free of typographical errors. Only a few have been noted, as on p. 46, "Pool"; p. 190, "hairiness" is the usual form of the word; on p. 192, the date after Menyanthaceae should be "1838"; and on p. 202 the rings should be "mestome."

This book is important to all interested in taxonomy and phylogeny of vascular plants. The fine quality of printing and paper give it an excellent physical make-up. The merits of the taxonomic scheme presented will of course become more apparent as the subject is studied further. In the words of Dr. Gundersen, "the phylogenetic arrangement adopted is only tentative, not to be accepted but to be improved."—GEORGE NEVILLE JONES, University of Illinois, Urbana.

NATIVE ORCHIDS OF NORTH AMERICA. By Donovan Stewart Correll. With illustrations by Blanche Ames and G. W. Dillon. Cultural notes contributed by E. T. Wherry and J. V. Watkins. Foreword by C. Schweinfurth. Published as volume XXVI of "A New Series of Plant Science Books," edited by Frans Verdoorn, 400 pages, 146 plates, and a number of text figures. Chronica Botanica Company, Waltham, Mass. 1950. $7.50.

This book, a beautifully illustrated taxonomic manual dealing with orchids, is not only one of the more useful and attractive botanical books produced in the past decade, but it is also the first botanical manual to include all species of orchids known to occur in North America north of Mexico. The book is written by a specialist. It includes 46 genera, 150 species, several varieties, and a number of hybrids, making a total of nearly two hundred kinds of orchids. Most of the illustrations are published for the first time. Combining, as it does, popular interest with botanical accuracy, this book is scientifically satisfactory and has also a wide popular appeal. The work has been brought to completion with the aid of a Guggenheim Fellowship granted to the author in 1946-47. It is based on the author's field work in several parts of North America, and on study of extensive series of botanical specimens from several of the more important herbaria. Dr. Correll expresses gratitude to the late Professor Oakes, founder of the Oakes Ames Orchid Herbarium, Harvard University, where the work was carried on.

The treatment of each species of orchid is begun with the valid binomial and the authority, followed by citation of the place of original publication. A useful feature is the statement of the type locality. There is a brief synonymy, but with places of publication omitted. The meaning of the technical name is explained, and a common name or names are provided. These items are followed by a detailed taxonomic description of the species. The discussions include miscellaneous information, and often some remark on distinguishing characters. As far as possible, complete geographical distribution is given for each species, although parenthetically, I note that Illinois, with its 32 species in 13 genera has been often overlooked, for less than a dozen orchids are directly attributed to Illinois, and one of these, *Cypripedium arietinum*, is probably not a member of the orchid flora of this state. The horticultural notes by Dr. Wherry and Dr. Watkins that are appended to the discussions of each species should be mentioned as one of the valuable features of the book, and the fact should not go without notice that there are excellent keys for identification of both genera and species. The book has a glossary of about 500 botanical terms used in descriptive orchidology, and for the benefit of the non-technical reader there is a list of the standard abbreviations of authors' names. There is a selected

bibliography of over 100 books and articles dealing with North American orchids, and two indexes, one for the scientific, and the other for the common names. There are many interesting items of information about orchids in the introduction and elsewhere throughout the book, as for example on page 2: "The number of seeds produced in an orchid capsule is in many cases phenomenal. The astronomers at the Greenwich Observatory, England, made an accurate count of the seeds in a capsule of the tropical American orchid *Cynoches chlorochilon* and found that it contained 3,770,000." And, on the next page: "Surprisingly, in recent years orchids have received political recognition. Minnesota has adopted the queenly *Cypripedium reginae* as its state flower. Brazil, Colombia, Costa Rica, Guatemala and Honduras have all issued postage stamps commemorating outstanding species prevalent in their respective geographical regions."

In the opinion of this reviewer, the Orchidaceae is the largest family of plants, with at least 18,000 species, although the author says it "is probably exceeded in number of species only by the Compositae." The taxonomy and nomenclature throughout the book appear to be sound and conservative, although the propriety of including the American yellow lady's-slipper in the same species as the Eurasian *Cypripedium calceolus* L., which is said to be represented in North America by the transcontinental var. *pubescens*, might be questioned. Dr. Correll has, however, discussed this subject at length in 1938. Two dozen species of *Habenaria* are grouped as one genus. And in *Spiranthes*, the second largest genus in North America, with 20 species, recent attempts to revive several very dubious Rafinesquian names have been commendably resisted. The arrangement of genera follows the modern phylogenetic scheme of Rudolf Schlechter (1926), and John Hutchinson (1934). The arrangement of species is alphabetical under the genera.

This excellent book, with its sound taxonomy, profuse illustration, high quality of printing, paper, and binding, and its remarkably moderate price, will undoubtedly serve as a valuable reference work, and will certainly stimulate interest in orchidology among naturalists and laymen generally as well as the professional botanists.—GEORGE NEVILLE JONES, University of Illinois, Urbana.

AN INTRODUCTION TO PLANT PHYSIOLOGY. By Otis F. Curtis and Daniel G. Clark. McGraw-Hill Book Company, Inc., New York. 1950. xi+752 pp. $6.50.

This textbook in plant physiology has been written for students who have at least a precursory knowledge of botany and inorganic chemistry. Those phases of the field (i.e., chemistry of photosynthesis, digestion, respiration and the metabolism of organic compounds) which require a greater background in organic, physical and bio-chemistry, are relatively under-developed. In the words of the authors: "Those interested in the biochemical aspects of plant physiology may feel that there is overemphasis on ecology and water relations, but we have found that these aspects of physiology are more easily developed without extensive preliminary training in chemistry and yet have an important bearing on horticultural and agronomic practices." In spite of these deficiencies the book serves well as an introduction to the subject of plant physiology. The discussion on water relations is one of the finest developed topics of the text. The interest of one of the authors, the late Professor O. F. Curtis, on the subject of solute translocation, makes its presentation (of 48 pages) one of the more valuable chapters.

Of special interest, since it emphasizes a rapidly developing area of plant physiology, is the chapter entitled "Conditions Influencing Flowering and Fruiting as Contrasted with Vegetative Growth." In this chapter the authors discuss, among other topics: the C/N ratio, control of flowering by temperature and photoperiod, photo- and thermoinduction, localization of regions sensitive to treatments and reason for response, light conditions previous to the dark period, temperature during the dark period, light intensity and wavelength, effect of the photoperiod on behavior other than flowering, and control by chemical treatment. This presentation marks the first appearance of many of these topics and concepts in a text book of plant physiology. The controversial topic of phasic development has been omitted.

The majority of the text figures on plant anatomy were supplied by Eames and MacDaniels from their text books. Many of the tables presented in the text were adapted by the authors to provide a clear presentation of their material. Each chapter has literature citations, general references and a set of questions and problems which the authors "have found useful for developing and understanding of basic facts and their applications to common problems of plant behavior." Some of these questions are answered or partially answered in one of the appendices. The other appendices are titled "False or Unsatisfactory Statements" and "Suggestions Relating to Completeness of Answers, Completeness of Proof, and Fallacious Reasoning."—EDWARD W. SYBIL, University of Notre Dame. Notre Dame, Indiana.

A NORTH CAROLINA NATURALIST. By H. H. Brimley. Edited by Eugene P. Odum. University of North Carolina Press, Chapel Hill. 1949. xvi+205 pp., frontispiece and 47 figs. $3.50.

Zoological collector, museum director, sportsman, poet, ardent conservationist, these and many other endeavors were a part of the life of Herbert Hutchinson Brimley.

Twenty-five of Brimley's papers are brought together by Dr. Odum to give us an entertaining view of this naturalist who adopted North Carolina for his home and activities. These papers, both published and unpublished, have in some instances been edited to fit the aim of the book, but mostly the thoughts and experiences of the man are reprinted as he wrote them. The six categories into which the volume is divided represent not necessarily a chronological presentation of essays, but rather logical groupings of Brimley's interests. Introducing each of these parts Dr. Odum gives a short background sketch which serves to tie the separate articles together and prepares the reader for the type of material contained therein. Occasionally, at the beginning of an article, one of Brimley's poems on an appropriate natural history subject introduces the article. As a poet Brimley was quite good; not only are his poems pleasant reading, but they embody a story and thoughts that in some respects give a greater insight into the man than his other writings.

The key to Brimley's philosophy is brought out in the last paper pertaining to the mounting of a whale skeleton, *we did what we could,* THEN, *with what we had!* This attitude perhaps more than any other was responsible for the accomplishments of the naturalist in any of his undertakings, be it egg collecting or directing the growth of a creditable state museum.

Dr. Odum reflects the influence of his former teacher in the preparation of this biographical sketch. All papers included have been thoughtfully selected, arranged, and introduced to give a composite of the versatility and nature of H. H. Brimley. This along with the good job of printing gives us an informative and enjoyable book about an informative and enjoyable person.—R. L. LIVEZEY, University of Notre Dame, Notre Dame, Indiana.

SELECTED INVERTEBRATE TYPES. Edited by Frank A. Brown, Jr. John Wiley and Sons, Inc. New York. 1950. xx+597 pages, 235 figs. $6.

This book, designed primarily as a laboratory manual, is the product of thirteen staff members of the Department of Invertebrate Zoology, of the Marine Biological Laboratory, Woods Hole, Massachusetts. They have made a definite contribution toward fulfilling the need of a manual for the general college course in invertebrate zoology. It is encouraging to note that this book contains a wealth of information concerning the selected types which serves to supplement the textbook material. This is a very desirable feature because it aids in achieving a higher degree of correlation between laboratory exercises and lectures. Also, the need of a new textbook for the general invertebrate zoology course is equally as great as the need of a laboratory manual.

There is no discussion of the higher categories since the book is restricted to represen-

tative species or genera. However, a complete classification is included in the table of contents. The illustrations are fairly plentiful and for the most part extremely clear. The references, including many monographs, considered by the authors and cited in the bibliography according to the subject matter are well chosen.

No doubt rigid limitations were necessitated in order to keep the book to a reasonable size and cost. Nevertheless, a number of the limitations and the selection of some of the types leave something to be desired particularly when fresh-water and terrestrial species are emphasized in an invertebrate course. The amphipods, isopods, notostracans, centipedes, scorpions and ostracods are not discussed. No fresh-water or terrestrial gastropod is included. Only one type of the various groups of rotifers is considered. Also, the large leech, *Haemopis grandis* (Verrill) or the native American medicinal leech *Macrobdella decora* (Say) Verrill would be a more desirable type than the European medicinal leech, *Hirudo medicinalis*.

The terminology to a specialist perhaps seems extremely simple, but the average college student is bewildered by the technical vocabulary used by invertebrate zoologists. For this reason an extensive glossary would be very valuable.

This book is a step in the right direction toward greater interest and better understanding of the invertebrates. It is highly recommended not only for the invertebrate zoologist but for the workers in related fields which demand a broad knowledge of representative invertebrate species.—CLARENCE F. DINEEN, University of Notre Dame, Notre Dame, Indiana.

OUR DESERT NEIGHBORS. By Edmund C. Jaeger. Stanford University Press. 1950. x+239 pp., illus. $5.00.

Edmund C. Jaeger has been studying and writing about the flora and fauna of our southwestern deserts for almost forty years. This book is his latest exposition in bringing the interesting desert organisms closer to the public, far too few of whom realize or respect the marvelous profusion existing in these "arid wastes." In this particular volume Mr. Jaeger is primarily concerned with the mammals and birds, but also has something to say about the lizards, snakes, tortoises, and a few arthropods.

At the outset the author gives some idea of the wealth of animal life to be found in a desert by citing what he has noted in one afternoon within a hundred foot radius of an exceptional example of Joshua tree. The next sixteen chapters are devoted to the mammals. Each of these chapters, as are most of those in the book, is limited to one particular animal and never is over nine pages in length. Undoubtedly the reader will find some of these too short. Personal experiences and observations are woven into very readable and entertaining narratives with scientifically accurate information of the animals' lives and ecology. Mr. Jaeger's style of writing is such that the uninitiated will not find the use of scientific names cumbersome or boring. His interpretation of *Ammospermophilus* as being "lover of sand and seed," and other similar explanations should encourage rather than deter the layman in acquaintance with these necessary words. The etymology is likewise explained in an entertaining way. There are also sixteen chapters about the desert birds; these follow the same pattern as those on mammals. The description of the discovery that the whippoorwill goes into a comatose state in winter, unlike any other known bird, is perhaps the highlight of this section. The next chapter treats of a few arthropods, the following of several desert lizards, then one on snakes, and the final chapter is on the desert tortoise. A selected list of references will guide those who wish to delve further into any of the forms contained in the book. There are thirty-three excellent photographs of desert life and nineteen fine-pen drawings, the latter used on the title pages of various chapters. The covers are similarly adorned with pen sketches and the end papers are maps of the desert regions of North America.

An appealing book for layman and professional biologist alike, *Our Desert Neighbors* should prove a welcome addition to any library.—R. L. LIVEZEY, University of Notre Dame, Notre Dame, Indiana.

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